THE PHYLOGENY AND MORPHOLOGICAL EVOLUTION OF CAMBRIAN TRILOBITES AND THEIR RELATIVES

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ABSTRACT

DESPITE abundant speculation about the nature and causes of the 'Cambrian explosion', there has been little empirical study of evolutionary patterns during this period. Understanding evolutionary patterns requires an explicit hypothesis of phylogeny. Empirical work has focussed on Cambrian arthropods and, in particular, on Cambrian trilobites. However, the phylogeny of these organisms is very poorly understood. This work investigates three major and long-standing problems in the phylogeny of Cambrian trilobites and their relatives. Implications of the phylogenetic hypotheses presented for understanding the 'Cambrian explosion' are discussed.

The suborder Ptychopariina includes a large proportion of Cambrian trilobite diversity and is ancestral to most post-Cambrian trilobites. Resolution of the phylogeny of the group is therefore central to understanding the trilobite radiation. Cladistic analysis is used to investigate relationships within the Cambrian ptychoparioid family Conocoryphidae, and to test claims that it is polyphyletic. Results indicate that the family consists of four distantly related clades.

Secondly, a new hypothesis of the relationships between arachnomorph arthropods is presented. This hypothesis is considered to be superior to previous cladistic studies in providing detailed discussion of homology and including a wider range of taxa. This analysis provides convincing synapomorphies for the Arachnomorpha and suggests that marrellomorphs are not arachnomorphs. The assignment of Cambrian megacheiran arthropods to the Arachnomorpha is confirmed and synapomorphies uniting them and chelicerates identified.

Finally, the evolution of the Agnostida is investigated. A number of synapomorphies uniting agnostids and eodiscinids are identified following detailed comparison of their morphology. The results of a cladistic analysis of 79 eodiscinids, representing almost all valid genera, and 3 agnostids indicate that the Agnostida consists of two major clades. The first includes weymouthiid eodiscinids and the Agnostina, the second includes yukoniid and eodiscid eodiscinids. Other eodiscinids form a basal paraphyletic assemblage. Preliminary taxonomic implications of this hypothesis are discussed.

For Helen

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AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the Regulations of the University of Bristol. The work is original except where indicated by special reference in the text and no part of the dissertation has been submitted for any other degree. Any views expressed in the dissertation are those of the author and in no way represent those of the University of Bristol. The dissertation has not been presented to any other University for examination either in the United Kingdom or overseas.

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1. INTRODUCTION

'The fossil record of Cambrian trilobites represents an unrivalled database for understanding aspects of the Cambrian radiation... the potential of this database remains far from being fully realized.' (Hughes 2001, p. 395)

THE 'CAMBRIAN EXPLOSION' is one of the most significant and controversial events in the history of life. There has been considerable speculation over the nature of this event, but comparatively little empirical evidence has been produced. Assessment of suggestions that unique evolutionary processes are necessary to account for the explosion requires detailed description of the pattern of morphological evolution during the Cambrian (e.g. Gould 1991; Wills *et al.* 1994). In particular, morphological evolution needs to be understood in a rigorous phylogenetic context (e.g. Wagner 1996, 1997).

Trilobites are increasingly recognized as the organisms of choice for investigating evolutionary processes during the Cambrian (e.g. Foote 1991; Hughes 2001). Trilobites are by far the most abundant Cambrian fossils, are morphologically complex, and their ecology and functional morphology can be understood by comparison with living arthropods. However, use of trilobites as a model for understanding Cambrian evolution is severely limited by the poor state of current knowledge of Cambrian trilobite phylogeny (Fortey 1990; 2001).

This work investigates, and makes important steps towards resolving, three major and long-standing problems in the phylogeny and systematics of Cambrian trilobites and their relatives. Namely, the phylogeny of the Order Ptychopariida, the relationships of trilobites to other arachnomorph arthropods, and the evolutionary origins of agnostids. The implications of the phylogenetic hypotheses presented for understanding morphological evolution during the Cambrian are investigated.

THE CAMBRIAN EXPLOSION

A diverse range of undisputed fossil Metazoa first appears more-or-less contemporaneously around the base of the Cambrian period, approximately 550 mya (Bowring *et al.* 1993; Landing *et al.* 1998). This so-called 'Cambrian explosion' or 'Cambrian radiation' is one of the most important and controversial events in the fossil record, and has been very widely reviewed (e.g. Bengtson 1995; Budd and Jensen 2000; Conway Morris 1992, 1998, 2000; Erwin 1994; Fortey *et al.* 1996; Geyer 1998*a*; McMenamin and McMenamin 1990; Sepkoski 1992; Signor and Lipps 1992*a*; Simonetta and Conway Morris 1991; Valentine *et al.* 1991; Zhuravlev and Riding 2001).

The earliest Cambrian fossils of the Nemakit-Daldynian and Tommotian stages (see Shergold 1997 and Zhuravlev and Riding 2001 for recent Cambrian correlation charts) constitute a characteristic boundary fauna known as the 'small-shelly fauna'. A few 'small-shelly' fossils are also known from the very latest Precambrian. These faunas consist largely of small mineralised structures, such as phosphatised tubes, cones and coils. These fossils seem to have few parallels among modern Metazoa, and their biological affinities are largely unknown. Comparisons have been made between these fossils and polychaetes, pogonophorans and molluscs, but are not generally accepted (Rozanov 1992). It is thought that some of these structures were sclerites covering the surface of a range of quite different animals (e.g. Bengtson *et al.* 1990). These animals or their scleritomes are almost impossible to reconstruct, except when very rare complete specimens are found, all of which are from later Cambrian deposits. For example, Tommotian sclerite-bearing animals may have resembled *Halkieria* (Conway Morris and Peel 1990) or *Wiwaxia* (Conway Morris 1985), flattened benthic crawling animals which may be related to molluscs and brachiopods (Conway Morris and Peel 1995), or *Chancelloria* (see Briggs *et al.* 1994), a (superficially) sponge-like scleritome bearing animal. The first fossils with clear affinities to later groups, including brachiopods (Popov 1992; Ushatinskaya 2001), sponges and archaeocyathids (Debrenne 1992; Debrenne and Reitner 2001), and possibly molluscs (Rozanov 1992), are also found in the small-shelly fauna.

In the next stage of the Cambrian, the Atdabanian, the first arthropods, in the form of trilobites (Briggs and Fortey 1992), and the first echinoderms, including helicoplacoids and edrioasteroids (Sprinkle 1992), appeared, and a radiation of both molluscs and brachiopods occurred. The first fossils of soft-bodied Cambrian animals are also of Atdabanian age, known from the earliest of the four major Cambrian fossil Lagerstätten, the Sirius Passet fauna of Greenland (Conway Morris *et al.* 1987; Conway Morris 2000) and the Chenjiang fauna of China (Hou *et al.* 1991; Chen *et al.* 1996, 1997). The faunas of these Early Cambrian Lagerstätten are very similar to that of the better known Middle Cambrian Burgess Shale (Briggs *et al.* 1994). The fourth fauna, the Upper Cambrian 'Orsten' of Sweden, shows a rather different mode of preservation and its fauna consists largely of tiny arthropods (Müller 1990; Walossek and Müller 1992, 1997, 1998; Walossek 1999). It seems that these exceptionally preserved fossils provide a view of a general Cambrian fauna. These faunas include taxa that have been assigned to nearly all the modern phyla that have any fossil record. In particular, a huge variety of soft-bodied arthropods has been found, and the now rare priapulids and onychophorans exhibited a great diversity. In addition to relatives of Recent groups, many Cambrian taxa exhibit character combinations unknown amongst post-Cambrian animals and, it has been suggested, belong to distinctly Cambrian phyla or classes (e.g. Conway Morris 1979*a*, 1982; Whittington 1980*a*; Gould 1989; Valentine *et al.* 1991).

It is not only animal body fossils that show a marked increase in diversity across the lower part of the Cambrian. A rapid increase in the complexity, diversity and abundance of trace fossils occurs at essentially the same time as the explosion in body fossil diversity (Crimes 1992*a*, 1992*b*; Jensen 1997). More recent revision of the Precambrian trace fossil record suggests that traces that can reliably be assigned to bilaterian metazoans are unknown from before the Cambrian (Budd and Jensen 2000). A decline in stromatolite diversity in the late Precambrian has been interpreted as the result of an increase in grazing and burrowing behaviour reflected in the trace fossil record (Valentine *et al.* 1991). Acritarchs and phytoplankton also show a radiation with a similar pattern to that of metazoan body fossils and trace fossils (Paliacos and Vidal 1992; Vidal and Moczydlowska 1992; Butterfield 1997).

The identification of numerous modern metazoan phyla in Cambrian soft-bodied faunas is in sharp contrast to the extensive soft-bodied faunas of the Vendian period of the Late Precambrian which contain no clearly metazoan taxa (Jenkins 1992; Fedonkin 1992, 1995; Narbonne 1998). These so-called Ediacaran faunas are now known from every continent except Antarctica, from about 620 to 550 Ma (Grotzinger *et al.* 1995; Jenkins 1995). The relationships of the members of these faunas have long been contentious. Many of these organisms have been considered to be primitive sister-taxa to modern groups. For example, Glaessner (1984) recognised members of a number of modern groups, including medusoid and pennatulacean cnidarians, flatworms, annelids and arthropods, and Durham (1978) suggested that members of the Cnidaria, Platyhelminthes, Porifera, Annelida, Mollusca, Arthropoda, Pogonophora, 'Conodontochordata' and the Echinodermata were all present in the Vendian. Some Ediacaran forms have been assigned to a variety of metazoan taxa. *Dickinsonia*, for example, has variously been regarded as a platyhelminth, a cnidarian (Valentine 1992), an annelid (Runnegar 1982*a*) and a unique kind of bilaterian (Fedonkin 1992). The reconstruction of these fossils as members of modern groups has, however, been contentious and assignment to metazoan taxa has generally relied on rather superficial features (e.g. Wagonner 1996). Two major problems have been the lack of evidence for mouths or guts in the frond-like and medusoid forms (Seilacher 1992), and the failure of body-divisions interpreted as metameric segmentation to meet across the mid-line of the fossils (see Signor and Lipps 1992*b*).

An alternative approach has been to regard the Vendian biota as essentially non-metazoan and none, or very few, of the organisms as ancestral to Cambrian or later animals. Seilacher (1989) suggested that these organisms represent a distinct 'evolutionary experiment' in multicellularity, and therefore do not belong within the Metazoa, but constitute a separate multicellular kingdom, the Vendobionta. He has since suggested (Seilacher 1992; Buss and Seilacher 1994) that many of the Vendian organisms may instead be the sister-group to other Metazoa (forming the phylum Vendobionta, or two phyla, the Vendobionta and Psammocorallia). Sielacher's view has been supported by taphonomic studies of Cnidaria and other taxa. Norris (1989) concluded that the Vendian organisms were very similar in form to

cnidarians, but must have been substantially stiffer than modern cnidarians (and particularly than medusoids or pennatulaceans) in order to account for the rareness of strongly folded or deformed Vendian fossils compared to the frequency of deformation during his experiments on dead Cnidaria. The structural simplicity of the Vendian fossils and cnidarians may also suggest that the observed body-form similarities are convergent (Seilacher 1992). A more recent suggestion has been that the majority of the Vendian organisms are lichens or fungi (Retallack 1994). The apparent diversity of Ediacaran fossils may largely be a taphonomic artefact. A single organism, consisting of a holdfast and frond, may have been capable of producing a range of frond-like, discoidal and bilaterally symmetrical fossils under different preservational conditions (e.g. Gehling *et al.* 2000).

In conclusion, most authors have accepted that the Vendian fauna included cnidarians, possibly of modern kinds (Conway Morris 1993). The affinities of the vast majority of these organisms, however, are unclear, and the ancestors of most modern groups do not seem to be present. The lack of obvious ancestors to later groups among these fossils suggests that the highly diverse Cambrian fauna originated rapidly, after the demise of the Ediacaran fauna (e.g Signor and Lipps 1992*b*, McMenamin and McMenamin 1990). The fossil record therefore seems to document the rapid origin of not only most extant metazoan groups, but also a wide range of animals that are unknown from post-Cambrian deposits during a short period at or around the Precambrian-Cambrian boundary. A number of attempts to quantify the magnitude of the Cambrian explosion have been made. Erwin (1994) suggested that the Vendian to Ordovician period produced all 11 of the recognised skeletonised marine phyla, 54 of the 56 recognised classes and 152 of the 235 orders. The majority of these appeared during the Early and Middle Cambrian. It has widely been suggested that all of the modern phyla may have originated during this period, even though many have left very little fossil record of any age (e.g. Valentine and Erwin 1987). Another study (Valentine *et al.* 1991) has listed 155 ordinal-level taxa that appeared during the Late Precambrian and Early Cambrian, 90 per cent. of which are extinct and 40 per cent. do not appear to belong to living phyla. Valentine and Erwin (1987) considered an estimate of 60 phyla (compared to approximately 35 living phyla, e.g.

Brusca and Brusca 1990) originating during the Cambrian explosion to be a very conservative one. Other authors have supported this view, e.g. 'as many as 100 phyla may have existed during the Cambrian, and only 5 percent or less of this number show evidence of a Precambrian ancestry' (McMenamin and McMenamin 1990, p. 168). All of these studies agree that species diversity in the Cambrian was very low in the vast majority of groups.

Explanations of the Cambrian explosion

A number of environmental changes have been identified at and around the time of the Cambrian explosion, and have been suggested as causing the event (see Signor and Lipps 1992*b*; Knoll 1996; Brasier and Lindsay 2001 and Eerola 2001 for reviews). It has been suggested that the Early Cambrian or Late Precambrian represented the first time that oxygen concentrations were sufficiently high to support complex animal life. The original evidence for low oxygen levels has been seriously disputed, and there is little reason to suppose that oxygen levels constrained evolution in the Precambrian (Signor and Lipps 1992*b*). Changes in carbonate, phosphate and carbon dioxide levels have also all been linked to the evolution of biomineralisation during the Cambrian (Signor and Lipps *op. cit.*). Changes in sea-level and continental shelf area have also been implicated in the Cambrian explosion (Brasier 1992; Lieberman 1999*a*). These may have been caused by tectonic changes, specifically the breakup of a late Proterozoic supercontinent, and/or by the termination of the Varangian glaciations (Rudwick 1964; Eerola 2001). The mechanism by which the lower sea-level and associated reduced area of continental shelf could significantly retard the evolution of the Metazoa is unclear, and Runnegar (1982*b*) has proposed the that the glaciations triggered the evolution of the Metazoa, rather than retarded it. Some of these environmental factors may have been involved in triggering the Cambrian radiation, but none could have controlled the pace or extent of the explosion. Environmental factors alone are therefore not sufficient to explain the suggested pattern of Cambrian evolution.

Attention has instead focussed on two possible biological explanations of the Cambrian explosion (see Valentine 1995; Foote 1996). It has been suggested by a number of authors that the Cambrian explosion represents the initial establishment of modern-style ecosystems (e.g. Valentine 1969, 1986; Paul 1979; McMenamin 1986; McMenamin and McMenamin 1990; Zhuravlev 2001), leading to rapid occupation of vacant ecological niches and correspondingly rapid morphological diversification. According to this 'ecospace hypothesis', the radiation of a few species very widely in ecospace followed by the elaboration of these basic body-plans throughout ecospace would result in the formation of higher taxa initially, with a subsequent increase in species diversity accompanied by little morphological radiation (Valentine 1986). Whilst early versions of this model assumed that the ecospace of possible niches was constant (Erwin 1992), a more plausible model would involve the origin of new niches during the occupation of ecospace, setting up the positive feedback of a true explosion (Erwin 1994). Testing of the 'ecospace hypothesis' has focused on the recovery from mass extinctions, which would be expected to show a similar pattern of diversification. For example, 95% of marine invertebrate species disappeared at the end of the Permian, and therefore Early Triassic ecosystems could be expected to be approximately as empty as Precambrian ones. During the recovery from the Permian-Triassic extinctions, however, very few higher taxa originated compared to during the Cambrian explosion (Erwin *op. cit.*). This has been explained as being due to the species remaining in the Early Triassic being widely spread out in ecospace, and therefore only short-range diffusion, re-establishing species diversity, was necessary to refill it.

Alternatively, it has been suggested that features of the early genome were responsible for the Cambrian explosion (Gould 1989, 1991; Valentine 1986, 1995; Valentine and Campbell 1975; Valentine and Erwin 1987; Valentine *et al.* 1996, 1999). One variation of this 'genomic hypothesis' is that the original setting up of metazoan developmental systems only reached a stage where complexity could rapidly increase in the Late Precambrian or Early Cambrian (Valentine 1986). Similarly, it has been argued that the Cambrian radiation may be linked to duplications of genes in the *HOM/Hox* cluster, allowing the evolution of greater

morphological complexity than smaller gene clusters (Valentine *et al.* 1996; 1999). Such suggestions are insufficient since they cannot explain why the rate of evolution subsequently reduced, without resort to other theories. For example, Valentine and Erwin (1987) argued that developmental or regulatory mutations provided the variation necessary for rapid morphological evolution, but that ecospace filling was responsible for controlling and halting the explosion. Interest has therefore focussed on the hypothesis that the Cambrian explosion was the result of lax developmental regulation in early genomes that subsequently became constrained (McNamara 1986; Gould 1989, 1991; Bard 1990). Under this theory rates of evolution fall as developmental systems become progressively less prone to advantageous mutation over time. Gould (1991) referred to this process as 'developmental canalisation'.

MORPHOLOGICAL EVOLUTION IN THE CAMBRIAN

Gould (1989) suggested that the large number of organisms in the Cambrian that cannot easily be accommodated within existing higher taxa represent bodyplans that are as distinct from each other as those of modern phyla and classes. Consequently morphological diversity (or disparity) was higher in the Cambrian than in more Recent times, despite low species-level diversity. This hypothesis suggests that there was something unique about evolution during the Cambrian explosion that resulted in more rapid morphological evolution per speciation event. This view is implicit in estimates of the magnitude of the Cambrian explosion by counting higher-taxa (e.g. Valentine 1986; Valentine and Erwin 1987) - Gould simply expressed it explicitly in terms of morphological disparity. Gould's presentation of a clear hypothesis of what was unusual about the Cambrian explosion has, however, lead to a welcome change in the nature of the debate. In contrast to the highly speculative nature of previous work (see especially numerous papers by Valentine and co-workers cited above), there has been a recent focus on empirically testing the reality of suggested evolutionary patterns.

Gould's (1989, 1991) model of the early origin of morphologically distinct higher taxa and the more traditional model of relatively gradual morphological evolution, with which he compared it are shown in Figure 1.1. The implications of these alternatives in terms of rates of evolution are considerable. In Gould's preferred 'decimation and diversification' model (Fig. 1.1B), the rate of morphological change is massively higher during the earliest branching events than later in time. In the more traditional increasing diversity model (Gould's 'cone of increasing diversity' - see Figure 1.1A), rates of evolution are more nearly constant over time.

The limitations of 'taxon counting'

The idea that the early occurence of many higher taxa indicates very rapid evolution depends upon the extent to which these taxa represent phylogenetic or morphological groups. In cladistic terms higher taxa can be identified as highly inclusive clades - major branches of the tree of life. More traditionally, higher taxa can be regarded as sharing a Bauplan, or fundamental bodyplan. It is unclear to what extent higher taxa currently recognised represent morphotypes and to what extent they represent major clades. For example, the traditional phylum Pentastomida is now thought to be a morphologically distinctive group of derived branchiuran or copepod crustaceans (Brusca and Brusca 1990) and therefore under cladistic logic should perhaps not be afforded even ordinal rank. These two ways of defining higher taxa have very different implications for the claim of rapid Cambrian evolution and maximal Cambrian disparity.

Under both the traditional model of gradually increasing disparity through time (Fig. 1.1A) and Gould's preferred model (Fig. 1.1B), higher taxa, if defined purely phylogenetically, would appear early in the history of the group purely because of the branching pattern of evolution (Raup 1983). Alternatively, if higher taxa are defined purely by morphological discreteness, these two models have very different implications for their origins. Under the 'cone of increasing diversity' model, the morphological distinctness of the major branches (higher taxa) is initially low, and increases gradually over time. This would lead to the gradual

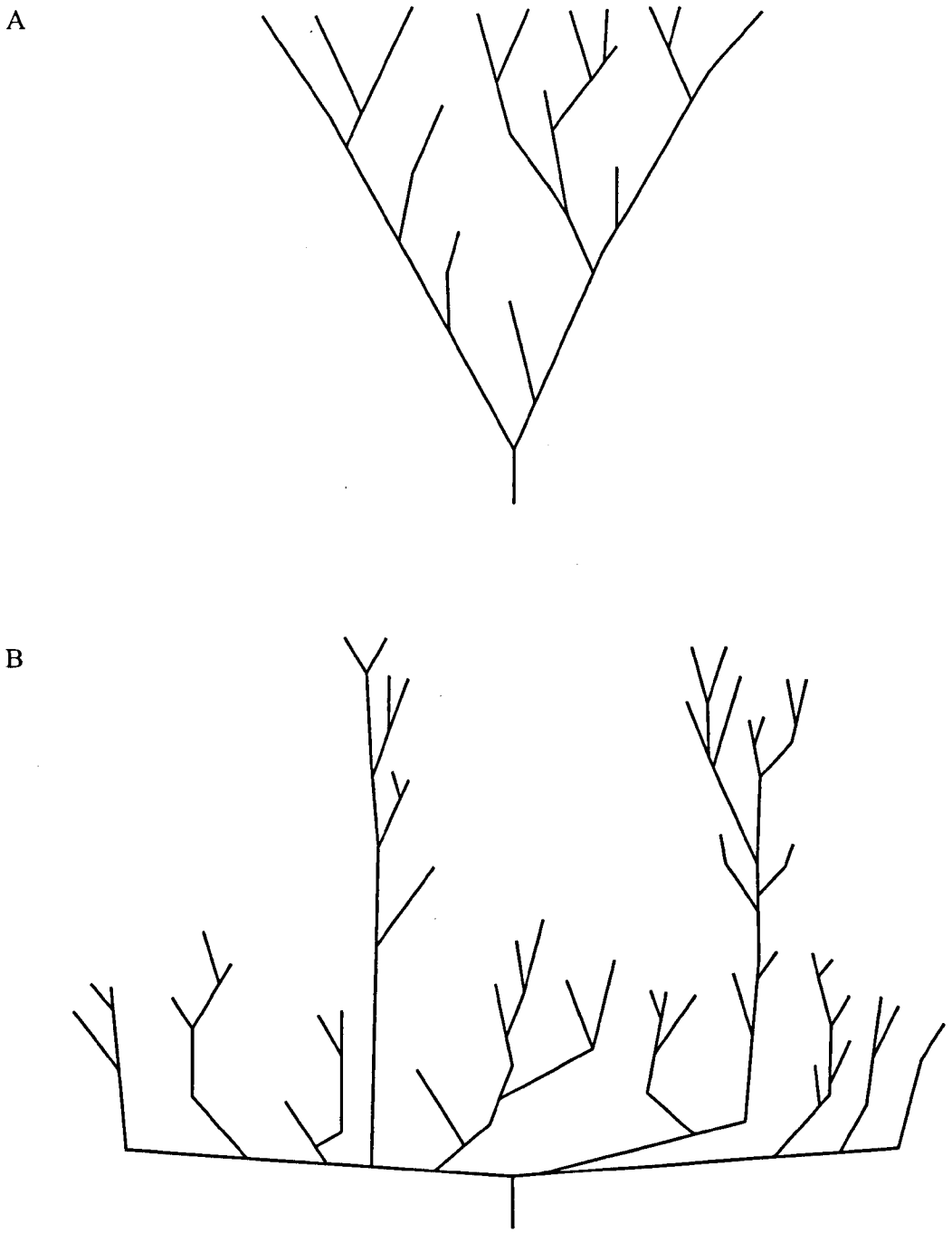


FIGURE 1.1. Contrasting models of evolution during the Cambrian explosion. A. Traditional view, the 'cone of increasing diversity'. B. Gould's (1989) hypothesis, the 'decimation and diversification' model. Redrawn from Gould (1989, fig. 1.17, p. 46).

formation of morphological distinct groups. In Gould's 'decimation and diversification' model, the morphological discreteness of major branches is established very early in their history, and does not change appreciably after their initial rapid origin.

Gould's model is therefore only supported if there genuinely is a larger number of higher taxa in the Cambrian, and these represent morphological units. There are a number of reasons to suppose that this might not be the case. Firstly, the idea that there was a huge number of extinct phyla or classes in the Cambrian may be an artefact of taxonomic practice. Primitive Cambrian members of extant groups may not have possessed many of the synapomorphies that define the modern groups, and may therefore incorrectly be considered to represent distinct taxa (see Gould 1991, 1993; Ridley 1993). Suggestion that up to 60 or 100 phyla may be present in the Cambrian (Valentine and Erwin 1987; McMenamin and McMenamin 1990) is suspect, when many of these organisms may be primitive members of modern groups. For example, the anomalocaridids have convincingly been shown to be arthropods (Budd 1996*b*, 1997, 1999*b*).

Conversely, Cambrian members of Recent phyla and classes may have been incorrectly recognised on the basis of single characters (Budd and Jensen 2000). Such taxa may be part of the stem-group of the taxon, below the origin of major features of the body-plan. Recognition of the phylum in the Cambrian on the basis of such species does not indicate that the distinctive body-plan that characterises Recent members of the group was established. For example, supposed polychaete annelids from the Burgess Shale (Conway Morris 1979*b*) lack important elements of the annelid body-plan, such as a peristomium and sclerotized jaws (Budd and Jensen *op. cit.*, p. 259). Assessment of the importance of particular characters in defining membership of taxonomic groups clearly requires cladistic analysis that includes fossil taxa (Briggs *et al.* 1992*a*, 1993). For example, cladistic analysis of arthropods has suggested that tagmosis patterns are not any better than many characters at defining major branches when Cambrian arthropods are included (Briggs *et al.* 1992*a*, Wills *et al.* 1994).

Even if higher taxa did only represent morphological units, and the number of higher taxa in the Cambrian was known, 'taxon counting' would still provide an unreliable guide to

morphological evolution. Firstly, the morphological distances between baupläne and the amount of morphospace occupied by higher taxa can both change (Foote 1991) and both could indicate important evolutionary changes. Secondly, there is likely to be considerable inconsistency in the use of taxonomic ranks between groups of organisms. A class of, for example, brachiopods, may not encompass the same degree of morphological variety as a class of molluscs. More importantly, similar inconsistencies may occur within groups. Organisms of a different age or geographical distribution are often studied by distinct workers, who may differ in their use of taxonomic ranks. The degree to which higher-taxon diversity gives an accurate impression of disparity has been quantified by Foote (1996). He concluded that in the Blastozoa and Crinoidea higher taxonomic diversity reflects disparity well over the Palaeozoic as a whole, but that in the Trilobita the correlation was much less good. More importantly in terms of the Cambrian explosion, Foote's data (1996, p.64, fig. 4.1) clearly shows that in both the Blastozoa and Trilobita, disparity and higher taxonomic diversity are not highly correlated during the Cambrian.

Studies of morphological disparity

Higher-taxon diversity clearly represents an inadequate proxy for morphological diversity, and as such, cannot provide a robust test of the hypothesis of unusually rapid morphological evolution during the Cambrian. This has led to a number of attempts to directly measure morphological disparity. Most such studies have concentrated on arthropods, and there has been widespread agreement that arthropods provide a good proxy for Cambrian metazoan disparity as a whole (e.g. Gould 1991; Briggs *et al.* 1992*a*).

Gould's claim has been directly tested by comparing the Burgess Shale arthropods with a range of Recent arthropods (Briggs *et al.* 1992*a*, 1993; Wills *et al.* 1994). This study used both cladistic and phenetic methods (see Wills *et al.* 1994) to investigate a data set of characters that could be preserved in a Burgess Shale setting. The authors concluded that the

range and variance of morphology of Cambrian arthropods were not significantly different to those of Recent arthropods. Their analysis also shows that, contrary to the claim of Foote and Gould (1992), Cambrian arthropods largely occupy morphospace intermediate between the four arthropod groups that survived the Cambrian (Briggs *et al.* 1992*a*, 1992*b*).

However, it has been suggested that the results of this study support suggestions of unusual evolutionary processes during the Cambrian explosion (Erwin 1994). According to these results, the occupation of morphospace was seemingly established very quickly in arthropod evolution and has remained largely constant until the Recent. An unusually high rate of evolution would be required to explain this rapid filling of morphospace, in accordance with Gould's (1989, 1991) rejection of the 'cone of increasing diversity' (Foote and Gould 1992). Both Foote and Gould (*op. cit.*) and Lee (1992) have suggested that this indicates constraints on morphological evolution after the Cambrian.

This debate illustrates the major limitation of Briggs, Fortey and Wills (1992*a*, 1992*b*; Wills *et al.* 1994) study. The suggestion of unusual patterns of morphological evolution relies not on the absolute level of disparity, but on the relationship between disparity and taxonomic diversity. In isolation, the pattern of high early disparity could be the result of increased rates of speciation with rates of morphological evolution per branching event constant, requiring no explanation in terms of unusual processes of morphological evolution.

This has led to investigations of the relationship between morphological disparity and taxonomic diversity (Foote 1990, 1991, 1992, 1993, 1996, 1999). However, these studies also suffer from problems in the interpretation of results. A wide range of potential explanations for discordance between disparity and diversity, such as selective extinction and speciation, are possible in addition to Gould's hypothesised secular changes in the rate of morphological evolution (Foote 1996). Adequate testing of the suggested pattern requires an explicit phylogenetic hypothesis, as is becoming apparent throughout the field of evolutionary biology (e.g. Coddington 1988; Harvey and Pagel 1991; Pagel 1994; Harvey *et al.* 1996). Optimizing morphological data (whether discrete or continuous) onto a cladogram provides a direct estimate of the relationship between morphological evolution and cladogenesis (e.g. McShea

1994; Smith 1994; Wagner and Erwin 1995; Wagner 1995, 1996, 1997; Sidor and Hopson 1998). This approach allows considerable precision in testing patterns of morphological evolution. For example, statistically significant changes in the length of branches can be localised to particular clades (Wagner 1997), branches of a particular age or topological depth (Wagner 1995, *op. cit.*), or associated with particular characters (McShea 1994; Wagner 2001). These differences in pattern clearly have important implications for hypothesis about the underlying process.

TRILOBITES AS MODEL ORGANISMS

Trilobites are the best known Cambrian fossils and 'the biomass of trilobites in scientific collections far exceeds that of all other metazoans put together' (Hughes 2001, p. 370). The abundance of trilobite specimens and described species is the simplest, but perhaps the most compelling, justification for the use of trilobites in studies of the Cambrian. '75% of known Cambrian species are trilobites...it is the availability of trilobites...that makes them useful for a case study in diversification' (Foote 1991, p.461).

Trilobites are also morphologically complex, and it is clear that morphologically complex organisms enable easier morphometric and cladistic analysis, because of the wealth of characters available. As well as being complex, trilobites are relatively morphologically conservative. This facilitates the recognition of homologous landmarks, allowing the use of continuous characters in morphometric analysis (see Gould 1991), but also facilitates cladistic analysis by allowing more certain hypotheses of homology, simplifying character coding. The ecological and functional significance of many characters can be understood by comparison with living arthropods (Fortey 1985, 1990*b*; Fortey and Hughes 1998; Fortey and Owens 1999*a*, 1999*b*; Hughes 2001).

Trilobites are the most abundant Cambrian fossils because of the calcification of their exoskeletons. Calcified trilobites almost undoubtedly form a clade (Fortey and Whittington

1989; Fortey 1990*a*; Fortey and Theron 1994; Edgecombe and Ramsköld 1999), and therefore the history of this monophyletic group can be followed relatively completely through the Cambrian. It can justifiably be claimed that 'trilobites are the only group for which the record of early diversification can possibly be read directly from the sequence of fossils' (Briggs and Fortey 1992, p.343).

Morphological evolution of Cambrian trilobites

These advantages have led to trilobites being widely used to study morphological evolution in the Cambrian. Foote (1989) studied changes in the occupation of a morphospace, defined by the Fourier coefficients of cranidium shape of North American trilobites throughout the Palaeozoic. This showed that the morphological range encompassed by trilobites increased through the Cambrian until the mid-Ordovician, but declined in the Upper Ordovician (Foote 1991). Analysis of higher taxa showed that within-group dispersion did not increase over time, but the discreteness of trilobite groups increased significantly. This was not due primarily to the tendency of groups to move away from one another in morphospace, but more due to the origin of new, morphologically distinct higher taxa (Foote 1989, 1990, 1991).

In comparisons of the pattern of morphological diversification of trilobites with that of taxonomic diversification, Foote (1993, 1996) found that disparity increased gradually through the Cambrian and Ordovician, whereas diversity, at all taxonomic levels, was highest in the Mid to Late Cambrian and declined gradually from then. Rarefaction analysis (Foote 1992) of the relationship between diversity and disparity in trilobites showed the existence of many species in the Cambrian that are small variations on a relatively limited array of morphological themes. Foote (1988) also found that Cambrian trilobite genera are short-lived compared to Ordovician genera, with the lower Ordovician showing a transitional pattern.

This pattern is in distinct contrast to that predicted by Gould (1989), which implies that branching events early in a clade's history involved larger morphological transitions than later

cladogenesis. Instead, Foote's studies suggest that during the Cambrian species of trilobite originated rapidly, but that morphological diversity was initially highly constrained. This implies shorter branches earlier in evolutionary history. A number of problems with Foote's study can be identified. Firstly, a number of his results are very sensitive to errors caused by the use of paraphyletic groups, and many Cambrian taxa are widely thought likely to be paraphyletic (e.g. Briggs and Fortey 1989; Fortey 2001). Secondly, Foote only used two time intervals in the Cambrian, 'the trilobite-bearing Early Cambrian' and 'the Mid-Late Cambrian'. The pattern within the Cambrian is therefore rather unclear. Third, cranidium shape may not necessarily reflect the overall pattern of morphological evolution in trilobites.

Foote's results could be explained by taxonomic over-splitting. Over-splitting compared to later trilobites could have been caused by the use of trilobites in Cambrian biostratigraphy. As Foote noted (1988, p.269) it is unclear whether 'Cambrian trilobites are useful for biostratigraphy because they have high turnover rates, or they have apparently high turnover rates because they are needed for biostratigraphy'. A number of trilobite workers have suggested the latter (e.g. Fortey 2001). Potentially, over-splitting would lead to a false inflation of diversity change over time, and render Foote's results compatible with the traditional model of 'the cone of increasing diversity'.

The possibility of over-splitting is illustrated by other studies of trilobite morphometrics. Hughes (1991; Labandeira and Hughes 1994), in a study of variation within a population of the Upper Cambrian genus *Dikelocephalus*, concluded that this genus had been massively oversplit and that only one species *D. minnesotensis* should be recognised. This was based on the pattern of continuous variation in a large number of characters. This species, Hughes concluded, shows a very large degree of intraspecific variation in a number of characters compared to other studies. He suggested that this was evidence that this Cambrian species possessed a developmentally flexible genotype, as suggested by Gould (1989). In another study, Hughes and Jell (1992) described a technique for the computer restoration of flattened fossils and its application to a trilobite fauna from the Middle Cambrian of Kashmir. Out of eight asaphid species described from this fauna, they concluded that seven belong to

one species, *Hundwarella personata*, and that this species shows considerable variation, as in *Dikelocephalus*. This study may indicate that taxonomic over-splitting may be very deep - as these species were previously assigned to different subfamilies. This may reflect even greater developmental flexibility in Middle rather than Late Cambrian trilobites, or could just be due to the problems of classifying tectonically deformed specimens (or partly due to both). The extent of possible oversplitting of Cambrian species is also provided by Foote's use of Cambrian genera as equivalent to Ordovician species, which gave the same result as the use of Cambrian species, this was found to be true in both the nearest-neighbour and rarefaction analyses (Foote 1990, 1992). The suggestion that many of the characters that had been used to falsely distinguish species of *Dikelocephalus* are frequently used to define other trilobite species, may again indicate widespread taxonomic error (Labandeira and Hughes 1994).

Investigation of development in a Silurian proetide has also suggested weakly canalised development (Hughes and Chapman 1995; Hughes *et al.* 1999). However, this is likely to be an adaptive autapomorphy, rather than the primitive retention of weak developmental regulation. This example shows that the pattern of developmental flexibility in trilobite evolution may not be a simple one and that there may be more complex selective pressures acting than a simple trend towards greater canalisation.

Two contradictory pictures of the pattern of morphological evolution in Cambrian trilobites can be identified, with radically different implications in terms of the size of morphological transitions in the Cambrian. Foote's (1990, 1991, 1993) findings of very rapid cladogenesis with slower increase in disparity suggest small morphological changes and high levels of homoplasy due to tight morphological constraint. Hughes's studies imply that diversity may have increased more slowly during the Cambrian, and that Foote's findings were due to taxonomic over-splitting – suggesting a pattern more in line with Gould's hypothesis. Hughes ((1991; Labandeira and Hughes 1994) has also suggested that Cambrian trilobites may have exhibited weakly canalised development, as suggested by some explanations of the Cambrian explosion. This view has, however, not been supported by analyses of patterns of intraspecific variation (Smith 1998; Smith and Lieberman 1999).

These rival explanations make distinct predictions about the distribution of branch lengths in evolution, which can be directly tested on the basis of explicit phylogenies. Such an approach would not only allow the pattern of branch lengths to be tested but also allows testing of potentially causal correlates of morphological patterns, such as ecology (e.g. Hughes *et al.* 1999). Cambrian trilobite phylogenies have also been used to test for unusual rates of speciation during the Cambrian explosion (Lieberman 2001), and investigate the role of tectonics as a driving force of Cambrian evolution (Lieberman 1999*a*).

Progress in Cambrian trilobite phylogenetics

Testing suggested patterns in the Cambrian explosion as a whole, and in the morphological evolution of trilobites in particular, requires reference to explicit phylogenetic hypotheses. Trilobite phylogeny remains rather poorly understood (Fortey 2001). Hence, improved knowledge of the phylogeny of Cambrian trilobites has been identified as a key limitation on understanding the Cambrian radiation (Hughes 2001, p. 395).

There is a broad consensus that the systematics of trilobites are far from being adequately resolved. In the first edition of the trilobite volume of the *Treatise on Invertebrate Paleontology* (Harrington *et al.* 1959, p. 145), Harrington remarked that 'a wholly satisfactory, natural classification of the trilobites is beyond possibility at the present moment'. This sentiment was echoed 38 years later upon publication of the second edition of the *Treatise* (Fortey 1997, p. 289). The relationships between Cambrian trilobites are widely regarded as particularly obscure (Whittington 1966; Fortey 1983, 1997, 2001; Edgecombe 1992; Hughes *et al.* 1999).

In his recent review of trilobite systematics, Fortey (1997) singled out four issues for special attention, namely the systematic position of the Olenellina, the problem of the Ptychopariina, the status of naraoiids and the position of Agnostina, all of which focus on Cambrian taxa. The first of these problems has received considerable attention recently, both

from the perspective of the monophyly of Trilobita (see e.g. Fortey and Theron 1994; Edgecombe and Ramsköld 1999) and the relationships of olenellids to other trilobites (Lieberman 1998, 1999*b*, 2001). This work investigates, and makes important steps towards resolving, the three remaining problems identifed by Fortey (1997).

The first part of this thesis addresses the problem of determining relationships within the most diverse Cambrian trilobite group - the Ptychopariina. Previously, it has been suggested that homoplastic evolution is rife within this group and consequently that cladistic approaches to studying their relationships of little utility (Palmer 1965; Sundberg 1994). Ptychopariids are the most diverse Cambrian trilobite group and ancestral to most post-Cambrian trilobite groups (e.g. Fortey 1990*b*, 2001), so errors in ptychopariid taxonomy may have had a profound effect on analyses of the pattern of evolution within Cambrian trilobites as a whole. Secondly, the position of trilobites within the arthropod clade Arachnomorpha is investigated. The relationships between members of this group and its limits have been controversial (e.g. Wills *et al.* 1995, 1998*a*; Hou and Bergström 1997; Edgecombe and Ramsköld 1999). Previous cladistic analyses have failed to suggest convincing synapomorphies either for the Arachnomorpha as a whole, or for subclades within it. Finally, the 'agnostid problem' is addressed in two ways. Most recent authors have supported the placement of the agnostids within the Trilobita (Fortey and Theron 1994; Wills *et al.* 1998*a*), and this is reaffirmed on the basis of detailed comparison of agnostid, eodiscinid and 'polymerid' trilobites. Secondly, the phylogeny of the Agnostida is analysed in detail on the basis of a large sample of eodiscinid and agnostid taxa. These issues are introduced in more detail in the relevant parts of this work.

In each case, a new phylogenetic hypothesis is proposed on the basis of computer-aided cladistic methods (see Smith 1994; Kitching *et al.* 1998). The implications of these hypotheses for systematics and for understanding morphological evolution during the Cambrian are also investigated. Specific methods are described and discussed where first used.

2. THE PHYLOGENY AND SYSTEMATICS OF BLIND CAMBRIAN PTYCHOPARIOID TRILOBITES

THE ptychoparioid trilobites (suborder Ptychopariina Swinnerton, 1915) have been described as one of the biggest taxonomic wastebaskets in palaeontology (Palmer 1958; Geyer and Malinky 1997). As currently recognized the group is explicitly paraphyletic, consisting of the primitive members of the trilobite subclass Libristoma which lack the synapomorphies of more derived groups (Fortey 1990). Whilst the scope of the group is reasonably well established, in that widely accepted and clear criteria for membership have been proposed, the relationships between constituent groups are extremely problematic. This difficulty has long been recognized (e.g. Rasetti 1951) and authors have often resorted to completely abandoning suprageneric classification within the group, and arranging genera alphabetically (Palmer 1954, Palmer *in* Palmer and Halley 1979; Rasetti 1963).

The most recent classification recognized 31 families within the Ptychopariina (Fortey 1997) but many, if not most, of these families are unlikely to be monophyletic (Fortey 1990). Diagnoses of higher taxa within the group are typically vague and extensively refer to structures as 'usually' or 'sometimes' being present, and to 'trends' and 'tendencies' towards certain states (e.g. Harrington *et al.* 1959). Most of the families and superfamilies have been extensively criticized (e.g. Ptychoparioidea and Solenopleuroidea: Rasetti 1954; Öpik 1967; Ahlberg and Bergström 1978) but none of the currently proposed alternative classifications has any clear phylogenetic justification. Geyer and Malinky's (1997, p. 633) recent diagnosis of the family Antagmidae, for example, explicitly 'does not include single characters that permit a direct identification of antagmids, and the concept of the family has largely to base [*sic*] on recognition of 'outgroups'. Despite the plesiomorphic nature of the character set, the group appears to represent a natural group'. However, the authors present no arguments or evidence that this is the case. Regional differences in taxonomy may also have had a profound effect on the profusion of poorly founded familial and suprafamilial taxa within the group.

Many geographically highly restricted, but morphologically undistinguished, families have been erected (e.g. Zhang, 1963; Zhang and Jell 1987), and there are major geographical differences in the use of family names that have subsequently been considered synonymous (e.g. Öpik 1967, p. 184; Geyer 1998*b*). These problems have long been recognized (e.g. Rasetti, 1948; Hennigsmoen, 1951; Stubblefield, 1959; Temple *in* Cowie *et al.*, 1967), and were extensively discussed by Rasetti (1972), who commented that (p. 43) 'among no less than 19 superfamilies admitted to the suborder Ptychopariina of the order Ptychopariida in the Treatise, the differences are so insignificant and vague (when not altogether non-existent), that one can find cases of trilobite genera placed in different superfamilies which are even synonymous (e.g. *Proaulacopleura* and *Aphelaspis*).'

The phylogeny of the ptychoparioids is of particular importance because they are thought to be ancestral to the majority of post-Cambrian trilobites (see Fortey 1990; Fortey and Owens 1997), and therefore occupy a crucial position in the phylogeny and radiation of the trilobites as a whole (see Fig. 2.1). Secondly, they are the most diverse Cambrian trilobite group (e.g. Harrington *et al.*, 1959, Romano *et al.*, 1993), and as such have great potential for revealing patterns of evolution during the trilobite radiation. The whole of the Ptychopariina is in need of detailed phylogenetic attention, but this is an enormous task due to the huge diversity of the taxon. One alternative approach would be to identify a small number of potentially useful characters and carefully analyse their distributions across the group, as has proved fruitful in a number of recent discussions of high-level trilobite phylogeny (e.g. Fortey and Chatterton 1988; Fortey 1990; Chatterton *et al.* 1994*a*). This kind of method is impractical in the case of the Ptychopariina, however, because few of the constituent taxa (families) are satisfactory and few useful characters have previously been identified. The numerous suggestions of extensive iterative evolution within the ptychoparioids (e.g. Palmer 1965; Sundberg 1994) would perhaps lead to this 'key characters' approach being poorly received, since, in the absence of a formal cladistic hypothesis, the selected characters could be interpreted as prone to convergence. Another possible approach, taken here, is to undertake a detailed analysis of a subset of the group with the aim of identifying characters and methods

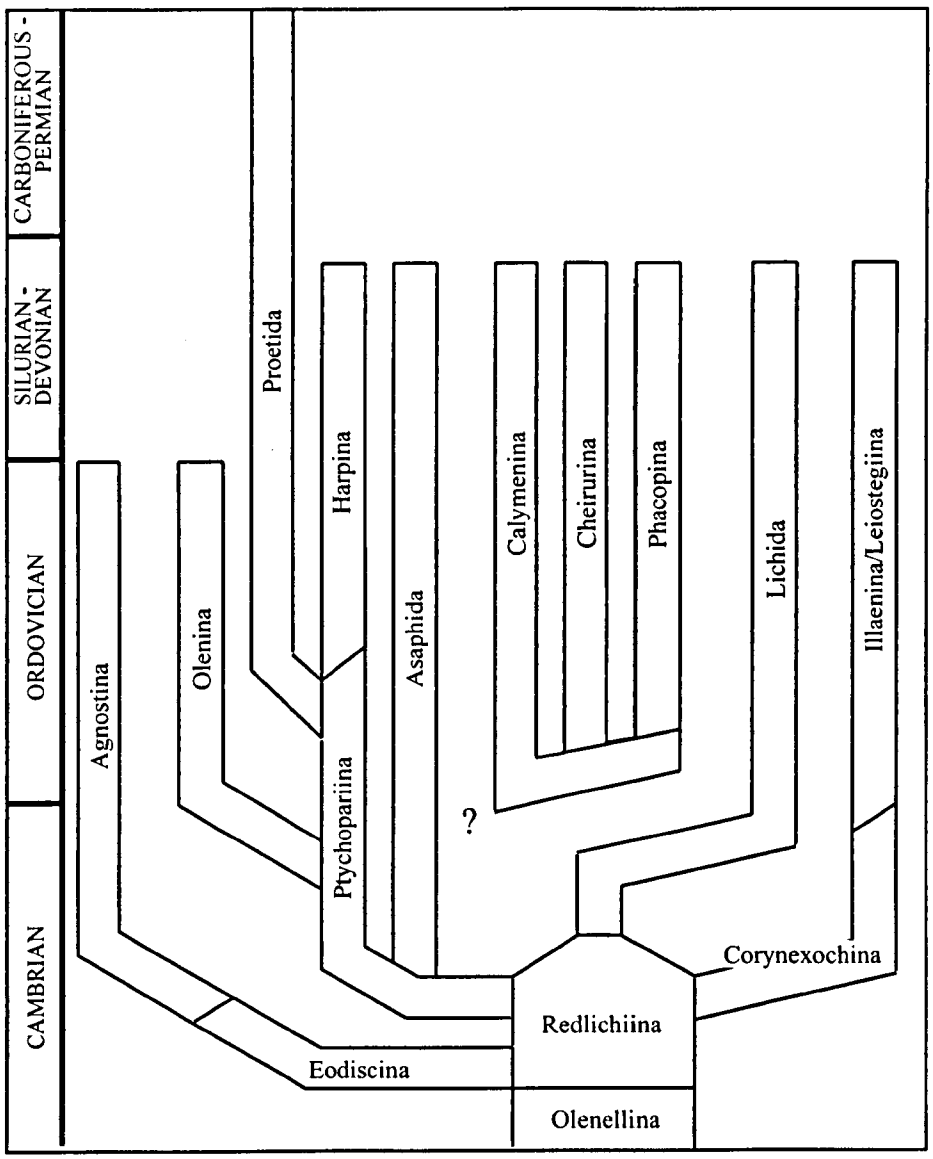


FIGURE 2.1. Summary of the phylogeny of trilobite orders and suborders, redrawn from Fortey (1990, text-fig. 19), illustrating the significance of the Ptychopariina in the evolution of post-Cambrian trilobite taxa, as a paraphylum ancestral to Asaphida (including Trinucleiodea), Harpina, Olenina, Phacopida and Proetida.

which can be used in a comprehensive analysis of ptychoparioid phylogeny. The application of cladistic methods to trilobites as a whole is still relatively rare (Adrain and Westrop 1999) and, in particular, there have been very few such studies of Cambrian trilobites (e.g. Hughes and Rushton, 1990, Babcock 1994*a*; Westrop *et al.* 1996; Sundberg and McCollum 1997; Lieberman 1998, 1999*b*, 2001). This study (most of which has been published in Cotton 2001) represents only the second application of formal cladistic methods to ptychopariid trilobites (following Sundberg 1999).

One of the very few families within the group that is presently diagnosed by a plausible monophyletic synapomorphy is the Conocoryphidae (e.g. Foote 1991, p. 476), which are united by loss of the eyes. However, many other instances of eye loss within the trilobites have been shown to be the result of convergence (e.g. Jell 1975; Fortey and Owens 1990; Clarkson 1997), and many authors have suggested that the Conocoryphidae may be polyphyletic, without proposing formal subdivisions. If the Conocoryphidae were to constitute a polyphyletic assemblage of blind ptychoparioids then detailed phylogenetic revision of the group should provide a useful illustration of characters and approaches capable of resolving other aspects of the ptychoparioid problem.

PREVIOUS STUDIES OF THE CONOCORYPHIDAE

Taxonomic history

The taxonomic history of the conocoryphids dates back to the earliest years of scientific trilobite study. The type species of the nominal genus of the family was assigned to *Trilobites sulzeri* by Schlotheim in 1823, but material attributed to this species was described over fifty years before this (see Šnajdr 1958). The family Conocoryphidae was erected in the middle of the nineteenth century (Angelin 1854), and a superfamily, then called Conocoryphidea, early in the twentieth century (Swinnerton 1915). Both these taxa have been used to include all the

current Ptychopariida or Ptychoparioidea (e.g. Swinnerton 1915; Richter and Richter 1941; Henningsmoen 1951), regardless of the presence or absence of eyes. More usually, they have been confined specifically to blind generalized ptychoparioids (after Stubblefield and Bulman 1927; Resser 1936) following the widely used classification of Harrington *et al.* (1959). Many authors have subsequently suggested that the family is polyphyletic. Lake (1940, p. 247), for example, commenting on the previous classification of Resser (1936), expressed some doubt that the genera *Dasometopus* and *Hartshillia* should be included within the family, and Westergård (1950) regarded only the genera *Conocoryphe*, *Bailiella*, *Bailiaspis* and *Ctenocephalus* as true conocoryphids.

The classification of Hupé (1953*b*, 1953*c*, 1955) represents the most extensive subdivision of the family to date. Hupé proposed the subfamily Hartshilliinae for the genera *Hartshillia* and *Hartshillina*, which he assigned to the Protolenidae (1953*a*, 1953*b*, 1953*c*), and the new family Atopsidae (1953*c*, 1955) for *Atops* and *Pseudatops*. He divided the remaining genera into four subfamilies of a reduced Conocoryphidae, which he still considered to be polyphyletic (1953*c*, 1955). Most subsequent authors also regarded the group as polyphyletic, but without suggesting alternative relationships (Hutchinson 1962; Rasetti 1967; Fortey 1990). Jenkins and Hasenohr (1989) suggested that the position of the facial suture on the brim is a key character defining 'true' conocoryphids, which on this basis would include *Atops*, *Conocoryphe* and *Hartshillia* (amongst others), but exclude *Bailiella* and *Bailiaspis*, implying a very different taxonomy to most other authors. Jell *et al.* (1992) distinguished between Lower Cambrian forms with a wide rounded glabella reaching the border furrow and Middle Cambrian forms with a 'ptychoparioid' glabella and pleural tips.

In contrast, very few authors have explicitly argued for the monophyly of the Conocoryphidae. In the most complete review of the family, Korobov (1973) did not discuss the polyphyly issue, but his discussion of evolution within the group (*op. cit.*, chapter 7) implies that he accepted the Conocoryphidae as monophyletic. A number of other authors have assigned taxa to the family without comment (e.g. Babcock 1994*a*).

The family Shumardiidae has previously been aligned (with doubt) with the Conocoryphidae to form the blind superfamily Conocoryphacea (Poulsen *in* Harrington *et al.* 1959), but this Ordovician group shows no particular similarities to the conocoryphids and is not considered further here. The genus *Hospes* Stubblefield *in* Stubblefield and Bulman 1927 has been included in the Conocoryphidae by some authors (Poulsen *op. cit.*), but has more recently been consistently assigned to the Shumardiidae (following Sdzuy 1955), and a large number of features support this assignment (Peng 1984, 1990; Zhou 1981).

Conocoryphid distribution

The Conocoryphidae ranges from the late Lower Cambrian through much of the Middle Cambrian (Korobov 1973). The family has a worldwide distribution in the Cambrian, and has been recorded from all of the major Cambrian continents. This wide geographic range is consistent with suggestions that the family is adapted to outer- or off-shelf environments (Lochman-Balk and Wilson 1958; Fortey 1990; Babcock 1994*b*; St. John and Babcock 1997). Blind trilobites are often associated with deeper-water conditions (Fortey and Owens, 1990, 1997). The absence of eyes in conocoryphids, along with some morphological features, such as a thin cuticle (Jenkins and Hasenohr 1989; Fortey and Wilmot 1991), of olenimorph (Fortey and Owens *op. cit.*) trilobites, which are also adapted to deep-water environments, supports the evidence from biofacies analysis. Cambrian polymeroid trilobites in general show strong facies dependence and geographic endemism (e.g. see Whittington, 1997*c*; Zhang, 1998; Palmer, 1998). If the family is shown to have an unusually wide geographic distribution, probably due to the potential for dispersal beneath a thermocline (Cook and Taylor 1975; Taylor, 1977; Babcock 1994*b*; St. John and Babcock 1997), then it may be useful in biostratigraphic studies.

Taxonomic scope

A phylogenetic analysis of 49 taxa was undertaken to determine relationships among taxa assigned to the Conocoryphidae, to test suggestions that the family is polyphyletic, and to assess possible relationships with non-conocoryphid taxa. Forty of the 49 taxa considered are currently assigned to the Conocoryphidae. These were selected to represent the morphological diversity present within the family, and include all of the validly described genera and subgenera. Where possible the type species of each genus was included, but where better material and/or descriptions of similar species were available, these were coded instead. Species that are morphologically distinct from the type species were also coded and, in most polytypic genera, more than one species was used so that potential generic synapomorphies could be determined from the analysis. All nominal genera assigned to the Conocoryphidae are represented with the exceptions of *Cainatops* Matthew, 1899, *Liaotungia* Resser and Endo *in* Kobayashi, 1935, *Liocephalus* Grönwall, 1902 and *Tangshiella* Hupé, 1953*b*. The status of these genera is discussed below.

Abundant missing data in cladistic matrices can lead to poorly resolved trees and to large numbers of equally most parsimonious trees (MPTs). It has therefore become common practice to exclude poorly known fossil taxa, with abundant missing data, from cladistic analyses (e.g. Sundberg and McCollum 1997; Lieberman 1998). However, such poorly known taxa may preserve unique character state combinations, and their *a priori* exclusion can result in incorrect hypotheses about the relationships of better known taxa (Wilkinson 1995*a*, *b*; Wilkinson and Benton 1996). Quality of preservation or description was therefore not used as a major criterion for omitting terminals in this study, unless superior data were available for very similar taxa.

Nine non-conocoryphid taxa were included in the analysis, selected according to previous hypotheses of relationships between conocoryphid taxa and non-conocoryphids.

Agraulos ceticephalus (Barrande, 1846) was coded following the suggestion of a relationship (Sdzuy 1961, 1966) between the Agraulidae and the conocoryphid genus *Holocephalina* Salter, 1864. The conocoryphid genera *Conocoryphe* and *Bailiella* closely resemble the 'generalized' ptychoparioids of the families Ptychopariidae, Solenopleuridae and Marjumiidae (Westergård 1950; Ahlberg and Bergström 1978, Fortey 1990; Geyer 1998*b*) which were represented by *Elrathia kingii* (Meek, 1870) and *Ptychoparia striata* (Emmrich, 1839). The recognition of a fused rostral-hypostomal plate in the conocoryphid *Hartshillia* (Hutchinson 1962; Lewis 1988), along with the anteriorly expanding glabella, makes a relationship with the Corynexochida possible. This was investigated by including *Olenoides serratus* (Rominger), and two blind corynexochids: *Clavigellus annulus* Geyer, 1994 and an undescribed new species of *Acontheus* from the Middle Cambrian of south-west Wales (described in an unpublished thesis by Lewis 1988, and to be formally described elsewhere). Relationships between the ellipsocephaloid ptychopariids and two conocoryphid groups: the Lower Cambrian conocoryphid *Atops* (Hupé 1955; Ahlberg and Bergström 1978), and the genera *Hartshillia* and *Hartshillina* (Hupé 1953*b*, 1953*c*; Sdzuy 1961), have been proposed. A generalized member of the Protolenidae (following Geyer 1990) was coded to assess these suggestions. This was coded with morphometric characters corresponding to the most frequent state within the family; other characters that vary within the family were coded as polymorphic. The advantages and disadvantages of representing higher taxa as terminals by using polymorphic coding compared to other methods of representing higher taxa (Bininda-Emonds *et al.* 1998) has not been assessed, and this is beyond the scope of this work. In this case, however, few of the characters were variable within the Protolenidae, this method of coding is therefore unlikely to have caused any major bias.

Two additional taxa were used as outgroups to determine character polarity: *Eoredlichia intermedia* (Lu) and *Olenellus* (*Olenellus*) *thompsoni* (Hall). These taxa are both widely accepted as outgroups to all the other taxa considered here. The Olenelloidea are considered to be the sister group to all other trilobites, and the Redlichiida a paraphyletic assemblage ancestral to all trilobites other than the Olenellina (Lieberman 1998; Fortey 1997).

TABLE 1. Authorship and important references for species included in cladistic analyses of blind ptychoparioids.

Atopina antiqua Korobov, 1966; Korobov 1973.
Atops rupertensis Jell *et al.*, 1992.
A. trilineatus (Emmons, 1844); Walcott 1886; Lake 1940; Howell and Stubblefield 1950.
Bailiaspis bobrovi Korobov, 1973.
B. dalmani (Angelin, 1854); Westergård 1950.
B. glabrata (Angelin, 1854); Westergård 1950; Sdzuy 1966.
B. venusta Resser, 1937; Hutchinson 1962.
Bailiella aequalis (Linnarsson, 1883); Westergård 1950.
B. baileyi (Hartt *in* Dawson, 1868); Matthew, 1885.
B. emarginata (Linnarsson, 1883); Westergård 1950.
B. lantenoisi (Mansuy, 1916); Zhang and Jell 1987; Jell and Hughes 1997.
B. levyi (Munier-Chalmas and Bergeron *in* Bergeron, 1889); Thoral 1946; Courtessole1973.
Conocoryphe caecigena Dean, 1982.
C. sulzeri (Schlotheim, 1823); Šnajdr 1958; Šnajdr 1982.
Cornucoryphe schirmi Sdzuy and Liñan, 1996.
Couloumania heberti (Munier-Chalmas and Bergeron *in* Bergeron, 1889); Sdzuy 1961; Courtessole 1973.
Ctenocephalus (*C.*) *bergeroni* Thoral, 1946; Courtessole 1973.
C. (*C.*) *coronatus* (Barrande, 1846); Šnajdr 1958.
C. (*Hartella*) *antiquus*;Thoral, 1946. Courtessole 1973.
C. (*H.*) *exsulans* (Linnarsson, 1883); Westergård 1950.
C. (*H.*) *matthewi* (Hartt *in* Dawson,1868); Matthew 1885.
C. (*H.*) *terranovicus* Resser, 1937; Hutchinson 1962.
Dasometopus breviceps (Angelin, 1854); Linnarsson 1883; Westergård 1950; Korobov 1973.
D. granulatus Korobov, 1973.
D. maensis Korobov, 1973.
Elyx laticeps (Angelin, 1851); Westergård 1950.
E. matthewi Hutchinson, 1962.
Hartshillia clivosa Lazarenko, 1965; St. John and Babcock 1997.
H. inflata (Hicks, 1872); Lake 1938; Lewis 1988 [unpublished].
Hartshillina spinata (Illing, 1916); Lake 1938; Lewis 1988 [unpublished].
Holocephalina leve Gozalo and Liñan, 1996.
H. primordialis Salter, 1864; Lake 1938; Hutchinson 1962; Lewis 1988 [unpublished].
Holocephalites incertus (Illing, 1916); Lake 1938; Zhou *in* Zhou *et al.* 1982.
Meneviella venulosa (Hicks, 1872); Lake 1938, 1940; Hutchinson 1962.
M. viatrix Shergold, 1973.
Parabailiella languedocensis Thoral, 1946; Courtessole 1973.
Pseudatops reticulatus (Walcott, 1890); Lake 1940; Howell and Stubblefield 1950.
Sdzuyella stremina Hajrullina *in* Repina *et al.*, 1975.
Tchaiaspis sdzuyi Korobov, 1966; Korobov 1973.
Tchaiaspis sp. nov. St. John and Babcock 1997.
Acontheus sp. nov. Lewis 1988 [unpublished].
Agraulos ceticephalus (Barrande, 1846); Šnajdr 1958.
Clavigellus annulus Geyer, 1994.
Elrathia kingii (Meek, 1870); Palmer 1954.
Eoredlichia intermedia (Lu); Zhang *et al.* 1980; Shu *et al.* 1995.
Olenellus thompsoni (Hall); Whittington 1989; Lieberman 1998.
Olenoides serratus (Rominger); Whittington 1980*b*; Sundberg 1994.
Protolenidae Richter and Richter, 1948; Geyer 1990.
Ptychoparia striata (Emmrich, 1839); Šnajdr 1958.

These outgroups were rooted at an internal node with a basal polytomy. Brief taxonomic details and some important references for the taxa included in this study are given in Table 1. Taxa are referred to by their current taxonomic assignment throughout the main body of this work. Where taxonomic changes are proposed, these are discussed in the Systematic Palaeontology section.

Characters and coding

Ninety-seven exoskeletal characters were coded. Descriptions of characters and character states are given in Appendix 1, and coding for each taxon in the data matrix in Table 2. Some characters are discussed in more detail below. All characters that were polymorphic within a taxon were treated identically to multistate coding representing uncertainty. This has no effect except on terminal branch lengths.

The coding of inapplicable characters in phylogenetic analysis is a difficult problem (Maddison and Maddison 1997; Wagonner 1996). Two methods have been used. Firstly, inapplicable character states can be coded as missing data. A complex structure may comprise characters: 'absent/present' and 'state1/state2', with taxa lacking the structure coded as absent for the first character and as missing for the second. Some authors have regarded this method as problematic because it may lead to reconstruction of impossible ancestral states, and hence unjustified trees (Platnick *et al.* 1991). The alternative is to code the second character as a third 'not applicable' state in taxa that lack the structure. This is problematic because it reduces character independence and effectively weights the inapplicable character. Waggoner (1996) accepted that using a separate inapplicable character state introduces unjustified weighting, but also suggested that coding as missing data is tantamount to discarding data. These views are inconsistent: coding a taxon as absent for one character codes all of the information about the complex character that is available, coding other states as inapplicable clearly codes this state again, and does not include any distinct

TABLE 2 (OVERLEAF). Data matrix used in phylogenetic analyses of blind ptychoparioids. Character numbers are shown at the top of the table; characters and states are described in Appendix 1 and the text. Missing data are indicated by a question mark, 'N' refers to non-applicable characters; other letters indicate multistate coding, as follows: A = {01}, B = {12}, C = {23}, D = {34}, E = {02}, F = {567} and G = {34567}.

	1111111111222222222233333333334444444444555555555566666666667777777777888888888899999999
	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567
Atopina antiqua	0N0000N000N00100??A003??10100??0001?????0B01102?0?0NN0NN0N0010????0N??????????????????0100N0??0
Atops rupertensis	0N0001N000N011000010030010400?10000111001020110210100NN0NN12101010200N??1621000110101B1?00000N0000
A. trilineatus	0N0001N000N0A10001100310100D00?10000111101020110 2?0?0NN0NN0N1010????0N??15200002?0102???00000N0000
Bailiaspis bobrovi	210001N000N0011111A0011101300A100001101011B?????0??01010N121010????0N??????????????????0000N0??0
B. dalmani	210000N000N00100122101110030001000111010111000110 0?01A11N?11010????0N??????????????????0000N0??0
B. glabrata	1N0001N000N000001220012B013100100001101 0?110001101?01011N0N000N????0N??????????????????0000N0??0
B. venusta	1N0000N000N0E100?33102B00031001000011 0?011A????A00?0101AN12101A????0N??????000100??????0000N?0?0
Bailiella aequalis	0N0000N000N02100?1C00111003000100011101011100??101?00012N1200??????0N???41N?????????????0000N00?0
B. baileyi	1N0000N000N02000?AC00211003100100011?1011B0001B0100A013N0N1010????0N????1N000??0?1020010000N0?00
B. emarginata	0N0000N000N02000123001CB0031?01000?1?01011A?????01?01012N0N101010100N??1???000100??????0000N???0
B. lantenoisi	0N0101N000N02000?2100111003 1?01000110?0111000110100012N0N10101?000N?131N000100?11B0010000N0000
B. levyi	1N0101N000N02?00??200???00310010000????0011 00??101?0A012N0N000N101?0N12131N000100BA0C0?10000N0000
Conocoryphe caecigena	0N000?N000N02000?1100112003110100 0?11010?10NNNNA0NN0A011N120010????0N???31N?????????????0010N?0?0
C. sulzeri	0N0000N000N020001A1001110130001000111010112000110100121 2N0N101010100N12131N000100210200 10000N0000
Cornucoryphe schirmi	0N0101N000N000001220011101311010000????1001100??10??00B12N111010????0N??????0000?0????0??0000N00?0
Couloumania heberti	0N0000N000N02000??100???003000100011101010120001A01?0A112N1210111??00N??131N000100210200 10000N0000
Ctenocephalus (C.) bergeroni	0N100?N000N02000??101???023000100001 10?0110NNNNA0NN122141121 01?10200N???41N000100??????0000N?0?0
C. (C.) coronatus	0N1001N000N02000?2101112023000100001101011 0NNNNA0NN122141111 01210200N12141N0001001?0?0?10000N?000
C. (Hartella) antiquus	0NA00?N000N00000??101???023000100011 0?0110NNNNA0NN022131121012????0N???31N?????????????0000N?0?0
C. (H.) exsulans	0N1001N000N000001110011201300010000110 1011B?10100??022131111011????0N??????????????????0000N0??0
C. (H.) matthewi	0N1000N000N00000?110011102300010000 1?01011100011?1?022131121012????0N??????????????????0000N0??0
C. (H.) terranovicus	0N1????000N00100?210011102300A1000?1101011 0NNNNA0NN02213112?01?????0N??????????????????0000N???0
Dasometopus breviceps	0N001N1100N0000000A000020030011001010020112100121 0?01014N10?00N????11???6??????????2101100000N0?00
D. granulatus	0N001N1100N00000?1A00A0A003001100?010020?1210??210?0101DN12000N????0N???6??????????????0000N0??0
D. maensis	0N001N1100N00000?AA0000A003001100100?0201121?01210?01014N10100N????10??162111011102101100000N0000
Elyx laticeps	0N0100N000N0011101A0011101300110000110101111001100?02113010101 0????0N??????0001?0???????0000N00?0
E. matthewi	0N0100N000N001001AA0010101300010001?0101?11101B0??022130111011????0N??????????????????0000N00?0
Hartshillia clivosa	0N0?1N0221?N0000040003??2?0NN20200?????10?0NNNN0NN0NN0NN0N010N0NNN0N??????????????????000N???0
H. inflata	0N0?1N02211N0000040003??2?0NN20100?????10?0NNNN00NN0NN0NN0N010N11000N01210N1112002010??1?000N?000
Hartshillina spinata	0N0?1N0221?N00000D0003??2?0NN20200?????01?0NNNN00NN0NN0NN0N010N0NNN0N01210N111300?0201?0?000N?110
Holocephalina leve	??0?1N02110N10000310012 10?31111110?????0000NNNN0?NN0001?N0N010N11000N???G201??000???????0000N?0?0
H. primordialis	20001N0110N11000021001110131111110?????0001100?110?00012N0N100N11110N???FB0A10100???????0000N00?0
Holocephalites incertus	??0?1N02011N000003100010000NN11000?????1000NNNN?1NN000??N0N010N112110???FB0110000???????0000N?0?0
Meneviella venulosa	20001N1000N10000011000010030011000010010112100121010101CN0N100N11200N??072011000102011100000N0000
M. viatrix	B?001NB000N10000001000010030 0A10000100101021001210?01013N0N000N10000N??07211101?102021100000N0000
Parabailiella languedocensis	0N0000N000N02000?1200???003A001000?110?0?10NNNNA0NN0A212N12101?10100N??131N0001001A0B0?10000N?000
Pseudatops reticulatus	0N0?1N0100N000000110021010400?100001111010201102 10?0NN0NN0N00101???0N???5????????????????1000N0??0
Sdzuyella stremina	??0?1N02110NA000?3100230010NN11000????0000?????000?000??N0N00??????0N??????????????????0000N0??0
Tchaiaspis sdzuyi	210?01N000N00101?0A0000002300A100000?01011B1101?0???NN0NN12101?????11??????????????????0000N0??0
T. sp. nov.	210001N000N0010111A0010001300A100000?0????0NNNNA?NN?1011N121012????11??????????????????0000N???0
Acontheus sp. nov.	0N0?1N0000N00000?4000300204??210?000?000000NNNN00NN0NN0NN0N010N0NNN0N01200N110B0?20021?01100N?110
Agraulos ceticephalus	20001N01111N1000043001120041 0?10100???1?10B100?000?0?010N0N000N11000N12151?0101000???11?0011?0000
Clavigellus annulus	??0????100N000000330031020 1?00100000???A0102000100 0?001?N0N000N10000N01??0?11?B0??102100?01110110
Elrathia kingii	0N0001N000N000000131010000410010000 1??000021001200000013N0N000N10000N12121?010A002103101001110000
Eoredlichia intermedia	0N001N2000N0000?013103111040001000011110012 00??10?10001?N0N000N11200N00142011020?10201?0011101001
Olenellus thompsoni	0N001N2000N00000020?030020300010000111?000200000000000011N0N?00N10000N00242100011?00??0??001101001
Olenoides serratus	0N0000N000N000000131032122 2?0?1000011?A01020001000?0NN0NN0N100N10100N011021110200210210000111100?0
Protolenidae	0N001N0000N000000131031010D00?10000111?0?020000000 10001?N0N100N10B00N??1F20000B00?0201?0001101000
Ptychoparia striata	0N0000N000N020000131011101410010001110101120001210000012N0N?00N10100N12A31N000100210400100111000 0

information. In this study, inapplicable characters are treated as missing data for most analyses because, due to the large number of such characters in the matrix, coding them as a distinct character state (and therefore heavily weighting them) could result in them dominating the analysis. However, the effects of this assumption were investigated by using a distinct character state in some analyses (see Results below), and they are shown as distinct to 'true' missing data (using the symbol 'N') in the matrix (Table 2). Unless otherwise stated, a coding of 'N' was treated as missing data, and identical to a coding of '?'. These methods are equivalent to Pleijel's (1995) coding methods C and B, respectively.

Considerable debate has also surrounded the use of quantitative characters in phylogenetic analysis (e.g. Chappill 1989; Rae 1998). The general case for the use of such characters is well established (Thiele 1993; Rae 1998), but a number of methods for coding them have been proposed, and there is no consensus as to which is most appropriate (see Thiele 1993, for a review). For this study, quantitative characters were coded informally. Large discontinuities in the distribution of a state between species were identified and used to form distinct character states. The number of character states for quantitative characters is therefore determined by the degree of discontinuity between species. This approach is intended to be similar to that used in coding discrete characters. Less conservative coding of quantitative characters, using a formal gap coding method (e.g. Mickevich and Johnson 1976), may have improved the resolution of the results, but would require a detailed consideration of levels of intraspecific variation.

Preservational control of character states is unlikely to have had a significant effect on the results of this study. Most of the taxa considered are known from undistorted material. The coding was conservative, resulting in a large amount of missing and multistate character coding (21.3% of all observations) in the data matrix. Many of the characters that are most susceptible to taphonomically induced variation (see Hughes, 1995) were found to have lower than average character consistency indices (see Appendix 2), and therefore little influence on topology.

Terminology for all characters described in Appendix 1 and below follows Whittington (1997*a*), unless otherwise stated. A number of characters warrant extended discussion:

Genal caeca and eye ridges. The presence of a system of radiating, anastomosing ridges on the frontal area and anterior genae of many trilobites has long been recognized (Öpik 1959, 1961*a*; Jell 1978), but the relationship between this system, the eye ridge and eye lobe has received little attention. In sighted trilobites with a prominent caecal system (e.g. *Harpides atlanticus* Billings; Whittington 1997*a*, fig. 17), a single ridge (the genal ridge) continues the line of the eye ridge beyond the eye lobe. It has been suggested that the thread-like eye ridge of blind trilobites (including conocoryphids) is homologous with this genal ridge and not the eye ridge of sighted forms (Whittington 1997*a*, p. 15). However conocoryphids have two distinct ridges across the genae, one usually lying over the other (Jell and Hughes, 1997, p. 62). In *Meneviella*, the putative eye ridge bifurcates adaxially, one branch running around the front of the glabella and the other inserting under the axial furrows, and abaxially, where two ridges follow separate paths across the posterolateral genae (Fig. 2.2A). In other taxa, such as *Bailiella baileyi*, the two ridges separate just outside the axial furrow, forming a low node (Fig. 2.2B). In other species, only a single ridge is visible. In *Bailiella emarginata*, this ridge terminates in the middle of the genae, and the caecal system is not evident. This suggests that the ridge in *B. emarginata* represents the eye ridge, and that the longer of the two ridges in other conocoryphids, which is associated with the caecal system, is absent in this species and is the homologue of the genal ridge of trilobites with normal ocular structures. The close correspondence between the prominence of the genal ridge and caecal system, which is lacking between the eye ridge and the caecal system, makes it likely that the genal ridge is part of the caecal system whereas the eye ridge is a separate structure. These two structures usually lie on top of one another and it is not always possible to distinguish between them, it may therefore prove useful to refer to them collectively as the genal ridges (as in Appendix 1). The function of the various caecal structures has been the subject of some debate (e.g. Öpik 1961*a*;

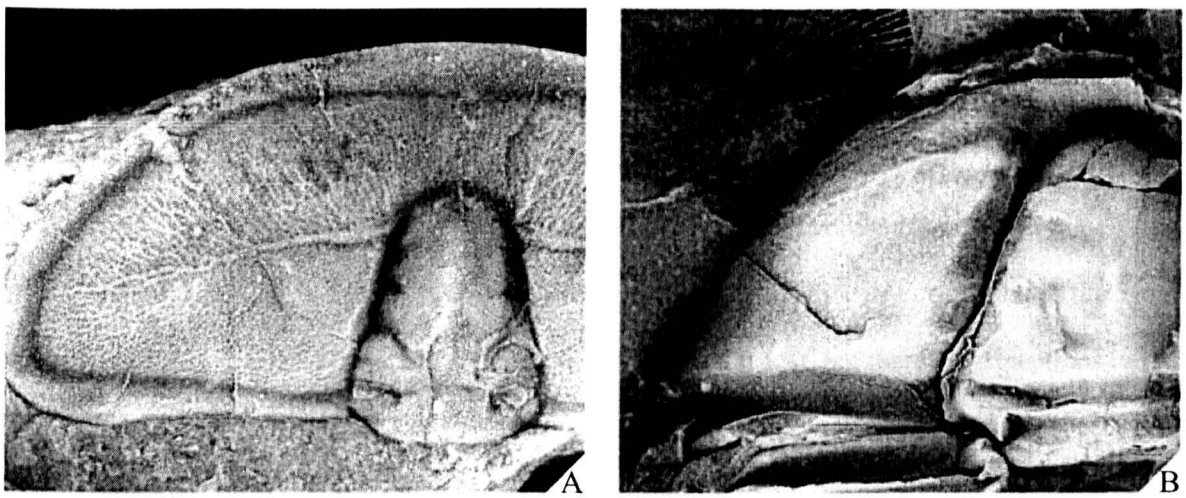


FIGURE 2.2. A, *Meneviella venulosa* (Hicks, 1872), BMNH It.13575; Middle Cambrian, *Paradoxides davidis* Zone, Manuel's Brook Formation, Manuel's Brook, Newfoundland; dorsal view of left side of cephalon; x6.5. B, *Bailiella baileyi* (Hartt, *in* Dawson, 1868), BMNH It.3951; Middle Cambrian, Fossil Brook Formation, Fossil Brook, St. Martins, New Brunswick; dorsal view of left side of cephalon; x3.2.

Bergström 1973; Fortey 1974; Jell 1978; Chatterton et al. 1994*b*). The interpretation of these structures argued here supports theories that two distinct organs are represented.

A number of characters of the eye ridge, genal ridge and caecal system are coded in this study. The presence of the (ventral with respect to the dorsal cuticle) caecal system on the external surface probably reflects a thinning of the cuticle. Its absence from internal moulds may indicate either a reduction of the caecal system itself or a change in the relationship between the caecal system and the cuticle. The insertion of the eye ridges into the glabella is variable (Korobov 1973). In some taxa raised ridges cross the axial furrows, and initially run anterolaterally (e.g. *Pseudatops reticulatus*, Pl. 2, figs 1-3). In other taxa the ridges do not interrupt the axial furrows and run directly laterally or posterolaterally (e.g. *Conocoryphe sulzeri*, Pl. 3, figs 9-10). The interruption of the axial furrows by the eye ridges may be of importance in separating the advanced ellipsocephaloids and ptychoparioids from more primitive ellipsocephaloids such as the Antatlasiidae and Protolenidae (Ahlberg and Bergström 1978). Finally, the caecal system is usually much weaker posterior to the eye ridge (e.g. *Papyriaspis lanceola* Whitehouse; Jell 1978, fig. 1A), but there are exceptions (e.g. *Meneviella venulosa*, Pl. 3, figs 1-2, 4).

Preglabellar boss. Conocoryphids show a number of unusual specializations of the anterior genae and preglabellar field. An inflated boss occurs on the preglabellar field of *Ctenocephalus* and *Elyx* within the Conocoryphidae, and is widely distributed within ptychopariids (Fortey and Hughes 1998). Fortey and Hughes (1998) suggested that the boss represents the brood pouch of a female dimorph. However, they failed to identify possible male dimorphs for the majority of *Ctenocephalus* species. Secondly, the geographical distribution of the dimorphic pair they postulated, *Ctenocephalus* (*Hartella*) *exsulans* and *Bailiaspis dalmani*, may be different; *Bailiaspis dalmani* occurs with a *Ctenocephalus* (*Ctenocephalus*) species in Britain in the absence of any species referable to *Hartella*. Furthermore, the stratigraphical ranges of the genera *Ctenocephalus* and *Bailiaspis*, as currently understood, are not closely congruent (Korobov 1973, figs 2-10). Finally, the boss in

some species of *Elyx* (e.g. *Elyx palmeri* Korobov, 1973, pl. 6, figs 1-1A) takes the form of a narrow, raised ridge which is unlikely to have functioned as a brood pouch. The hypothesis of Fortey and Hughes (*op. cit.*) warrants further attention, but the evidence for a brood pouch in the conocoryphids is, at best, equivocal. The presence of the preglabellar boss was not treated as sexually dimorphic in this analysis.

Preglabellar furrows. Diverging preglabellar furrows, which can be considered as a distinct, novel structure or as anterior extensions of the axial glabellar furrows, are present in a range of conocoryphid species, including the type species of the nominal genus *Conocoryphe sulzeri* (Pl. 3, figs 9-10). In these taxa, the preglabellar furrows run from the anterolateral margins of the glabella to the continuous anterior border furrow. Furrows are also present in a similar position in some *Bailiaspis* species (e.g. *Bailiaspis menneri* Korobov, 1973, pl. 9, fig 4) and *Tchaiaspis sdzuyi* Korobov, 1966 (Pl. 4, fig. 9). These are not considered to be homologous to the arrangement in *Conocoryphe* or *Ctenocephalus*, but instead to represent an extreme development of the inward curving of the border furrow present in other *Bailiaspis* species. This is shown by the absence of a border furrow between the anteriormost points of the furrows, and the smooth connection of these furrows with the lateral border furrow. The arrangement of preglabellar furrows in *Elyx* (e.g. *Elyx trapezoidalis* Babcock, 1994*a*, fig. 8; *Elyx laticeps*, Pl. 4, fig. 6) is considered to be homologous with that in *Ctenocephalus*. A very faint border furrow divides the boss from the border, at least in some species, and the junction between the preglabellar furrows and the lateral border furrow is angular.

Anterior genal ridges. Posterolaterally directed ridges are present on the anterior genae of members of the subgenus *Ctenocephalus* (*Ctenocephalus*) (Pl. 4, figs 5, 8). These have been treated as homologous to the eye ridge (e.g. Hutchinson 1962), but most authors (Lake 1940; Courtessole 1973) have recognized them as distinct structures, since they usually consist of a ridge and a furrow, and do not meet the anterolateral corners of the glabella. The form of these structures, and their often extreme elevation above the ventral margin of the cephalon, also

indicates that they are distinct from the paradoublural line present in some species of *Dasometopus* (e.g. *Dasometopus maensis* Korobov, 1973, pl. 5, figs 1-4).

Hypostomes. The ventral morphology is known in very few conocoryphid taxa. Hypostome condition is coded following the terminology of Fortey and Chatterton (1988) and Fortey (1990). The form of the hypostome is not coded in detail, but a number of taxa share the conservative natant morphology ('generalised ptychoparioid form' in Appendix 1, character 71) identified by Fortey (1990, p.551, text-fig. 11).

Prosopon. It has been a widespread assumption in trilobite systematics that the pattern of sculpture or prosopon (following Gill 1949) is of 'low taxonomic value' and can be used, at best, to distinguish species, but not higher taxa. Prosopon is coded here alongside other characters, since its taxonomic value, at least in the group in question, has not been tested phylogenetically, and ignoring prosopon would amount to *a priori* weighting of characters.

Methods

Two distinct sets of analyses were performed. The initial analyses included only taxa that have been assigned to the Conocoryphidae. The matrix used in these analyses excluded the last 9 taxa, and characters 89-97, shown in Table 2. The second set of analyses used all the taxa and characters shown in Table 2. Analyses were carried out using PAUP* version 4.0b2a (Swofford 1999). Unless otherwise stated, all analyses used heuristic searches with 50 random addition sequence replicates. The software packages MacClade version 3.07 (Maddison and Maddison 1997) was used for comparing tree topologies and investigating patterns of character evolution. Tree statistics were calculated by PAUP* and checked with MacClade.

Quantitative characters, and those dimensions that were coded as discrete characters (i.e. those that could have been coded as quantitative characters), were treated as ordered in

the main analyses. The effects of this decision were investigated by reanalysing the data using different sets of character ordering assumptions. These sets were: (1) all characters unordered; (2) quantitative characters (as above) and those coding the degree of effacement of various structures treated as ordered; and (3) as above with characters coding other shape changes where intermediate states are plausible (Wilkinson 1992) added to the set of ordered characters. These sets of characters are shown in Appendix 1.

A number of authors (e.g. Sundberg and McCollum 1997; Sundberg, 1999) have advocated the reweighting of multistate characters so that the total weight of each character is equal, rather than the weight of each transition equal. The latter is more appropriate since multistate characters can be coded as an equivalent number of binary characters (e.g. Pleijel 1995). When coded in this way, each transition of a multistate character becomes a distinct binary character and is hence accorded equal weight. In most analyses all characters were treated as of equal weight, but the effects of this assumption were tested in some analyses by reweighting continuous multistate characters (those ordered in the first, or 'quantitative', character set described above and in Appendix 1). In these analyses multistate characters were reweighted so that the range of states had the same total weight in each case, e.g. characters with four states were downweighted to a third of the weight of binary characters, those with five states to a quarter. The weight of binary characters was maintained as one throughout.

Support for individual nodes was assessed by bootstrap analysis (Felsenstein 1985) and by calculating Bremer support indices (Bremer 1988, 1994). These methods measure two distinct aspects of support for phylogenetic hypotheses. Trees or nodes may be considered well supported (1) to the extent to which alternative topologies are much less parsimonious, as measured by the support index (Wilkinson 1996), or (2) where they are consistent with a large proportion of characters, so that character sampling is unlikely to have had much influence on topology, as assessed by bootstrapping (Page 1996). Bootstrapping was performed with 100 bootstrap replicates, each of ten addition sequence replicates. Support indices are also based on heuristic searches with ten addition sequence replicates.

Results

Analysis of taxa assigned to the Conocoryphidae. Initial analysis of the conocoryphid-only dataset (40 taxa and 88 informative characters) recovered 14 equally most parsimonious trees (MPTs), 301 steps in length. The midpoint rooted majority-rule consensus tree is shown in Figure 2.3. This midpoint rooting is also the most stratigraphically consistent (*Atops*, *Atopina* and *Pseudatops* are Lower Cambrian, whilst other conocoryphid taxa are Middle Cambrian, Korobov 1973), and results from outgroup rooting with *Eoredlichia intermedia*. The consistency index (CI) of these trees is 0.442, and the retention index (RI) is 0.712. Three major clades within the Conocoryphidae are easily recognized on the basis of this analysis, in that they are well supported, and subtended by long branches. The first (subtended by node 1 on Fig. 2.3) consists of the genera *Atopina*, *Atops*, and *Pseudatops*, the second (node 26) of *Dasometopus*, *Hartshillia*, *Hartshillina*, *Holocephalina*, *Holocephalites*, *Meneviella*, and *Sdzuyella*, and the third (node 5) of the remaining taxa.

Changes in the levels of resolution and support (as measured by the support index) when various taxa are excluded from the analysis can be used to identify problematic clades or terminals of uncertain phylogenetic position. The exclusion of *Hartshillia* (two taxa) and *Hartshillina* from the analysis resulted in a set of 131 MPTs of length 266 (with uninformative characters excluded). The shortest trees not showing the second major clade (node 26, without *Hartshillia* and *Hartshillina* in this case) in this analysis were 269 steps long. This gives a support index of three for this node compared to the index of two in the analysis including all taxa. Similarly the support index for node 31 increases from three to five when *Hartshillia* and *Hartshillina* are excluded. The reduced support for these clades when all taxa are included shows that the position of *Hartshillia* and *Hartshillina* is less certain than that of the other members of this clade.

Similarly, both the lack of resolution in the strict consensus tree, and the low support indices within the third major clade (including *Conocorpyhe*, *Bailiella*, *Bailiaspis* and

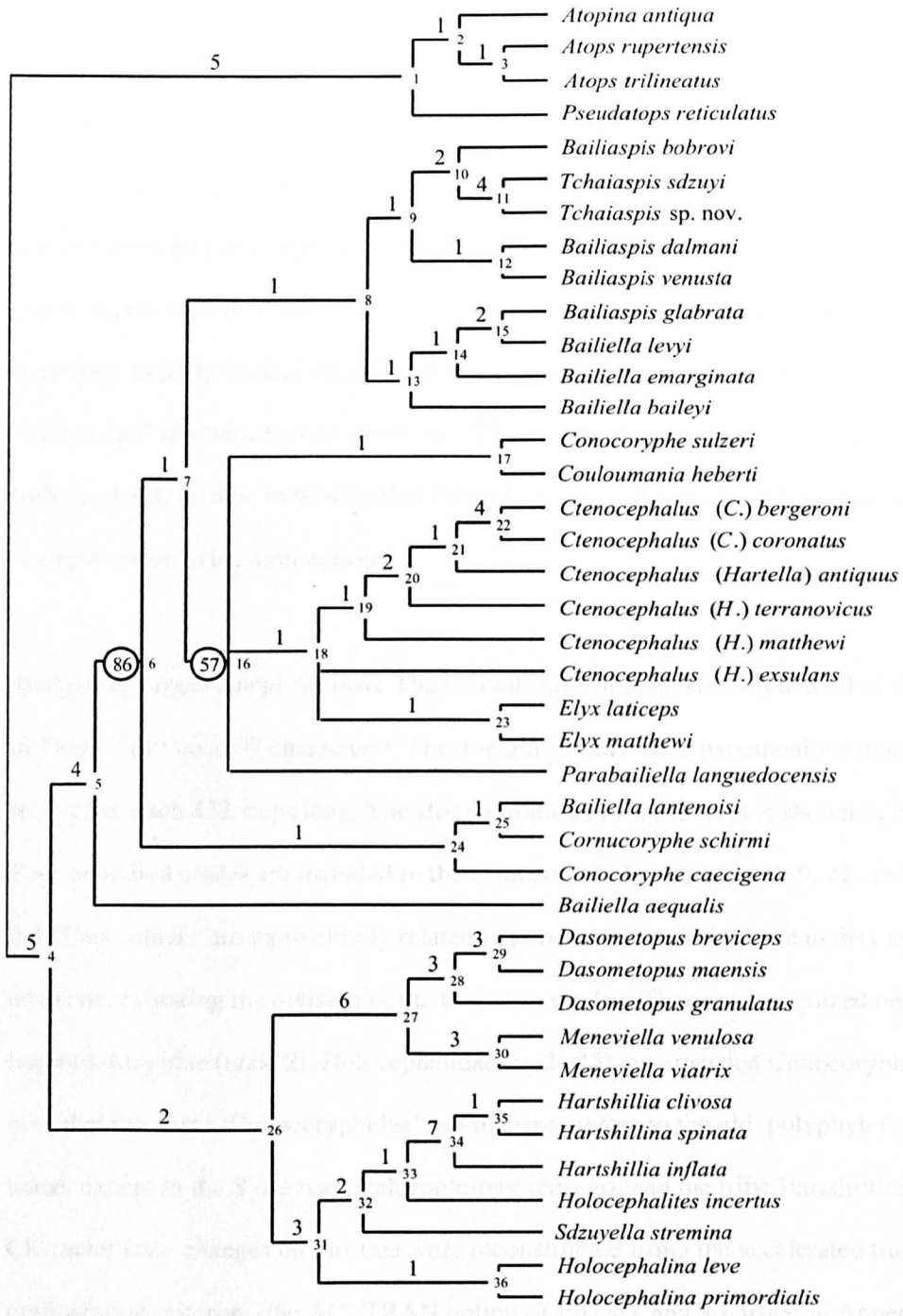


FIGURE 2.3. Majority-rule consensus tree resulting from analysis of conocoryphid-only matrix (see text). Numbers within circles over branches indicate the percentage of MPTs in which the clade occurs, for clades not present in all MPTs. Numbers in small type over nodes are node numbers, referred to in the text. Support indices are shown in bold type above branches.

Ctenocephalus, node five), may be a result of uncertainty about the correct position of a small number of terminals. This possibility was investigated by reanalysing the data without some terminals. Exclusion of *Parabailiella languedocensis* resulted in two trees of length 299, compared to the 14 equally parsimonious trees obtained when it was included. Exclusion of *Ctenocephalus* (*Hartella*) *exsulans* and *Parabailiella languedocensis* results in a single most parsimonious tree 294 steps long. The robustness of these results was also assessed by exploring the effects of different weighting and assumptions. The data were reanalysed separately treating each of the three sets of characters discussed above (see Appendix 1) as ordered, and all characters as unordered. These analyses gave similar (although generally less well resolved) results, indicating that the tree shown in Figure 2.3 is highly robust with respect to character ordering assumptions.

Analysis of larger sample of taxa. The second stage of analysis included all of the data shown in Table 2 (49 taxa, 97 characters). Thirty-eight equally most parsimonious trees were recovered, each 432 steps long. The strict consensus of these trees is shown in Figure 2.4. Four unrelated clades are included in the Conocoryphidae, at nodes 2, 9, 22, and 25 on Figure 2.4. These clades are more closely related to non-conocoryphid taxa than they are to each other, necessitating the division of the Conocoryphidae. They are recognized below as the families Atopidae (node 2), Holocephalidae (node 25), an emended Conocoryphidae (node 9; note that the name 'Conocoryphidae' in this paper refers to the old, polyphyletic, use of the name, except in the Systematic Palaeontology section), and the tribe Hartshillini (node 22). Character state changes on this tree were reconstructed using the accelerated transformation optimization criterion (the ACCTRAN option of PAUP), and are listed in Appendix 2. Accelerated transformation was preferred to other optimization criteria because it maximizes the interpretation of homoplasy as reversals, rather than as parallelisms, and hence minimizes rejection of the initial hypotheses of homology made during coding (Pinna 1991). The hypothesis of conocoryphid polyphyly is well supported by this analysis; the shortest tree compatible with conocoryphid monophyly is 456 steps long, 26 steps longer than the MPTs.

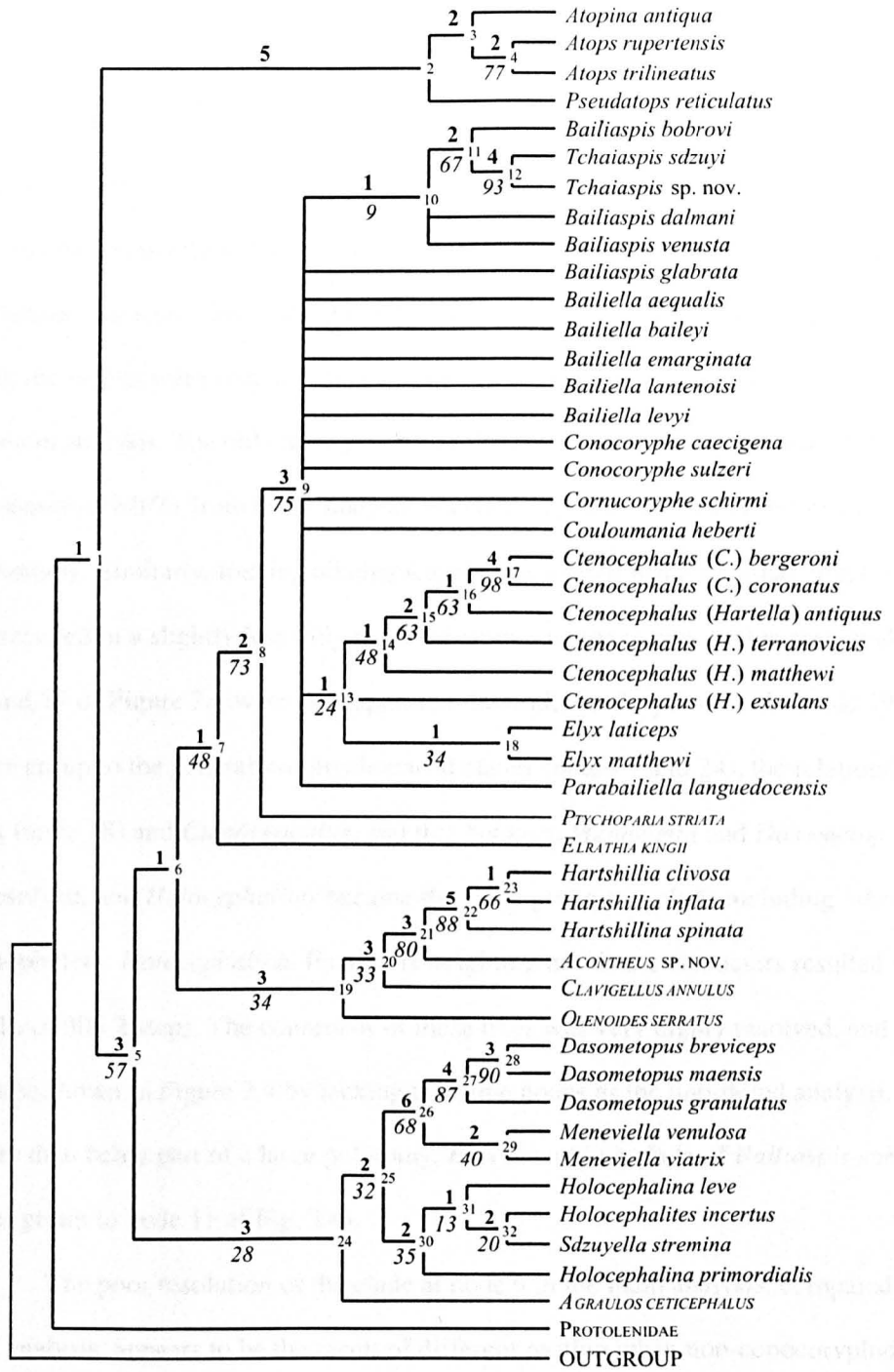


FIGURE 2.4. Strict consensus tree from analysis of complete matrix (see text). Numbers in small type over nodes are node numbers referred to in the text and Appendix 2. Support indices are shown in bold type above branches. Bootstrap percentages are shown in italic type below branches, for all nodes with relative frequencies greater than 5 per cent.

One hundred per cent. of bootstrap replicates supported conocoryphid polyphyly, support indices and the results of bootstrap analysis are shown on Figure 2.4.

Alternative assumptions about character weights and ordering were investigated for this larger database, as for the smaller one. The four clades identified in the main analysis emerged when either of the two alternative character sets were ordered, when all characters were treated as unordered, and when only the main set of characters was ordered and multistate characters down-weighted. When the alternative sets of ordered characters were used, the results were very similar to, but much more highly resolved than, those obtained in the main analysis. The only node present in Figure 2.4 that was not present in the strict consensus of MPTs from these analyses was node 23, the Hartshillini instead forming a trichotomy. Similarly, treating all characters as unordered had a minimal effect on topology, but resulted in a slightly less fully resolved strict consensus tree. In this case, nodes 6, 13, 29, 31 and 32 of Figure 2.4 were not supported. Instead, the Corynexochida (node 19) formed a sister group to the generalized ptychopariid clades (nodes 7 and 24), the relationship between *Elyx* (node 18) and *Ctenocephalus*, and that between *Meneviella* and *Dasometopus*, were unresolved, and *Holocephalites* became the sister group to a clade including *Sdzuyella* and a monophyletic *Holocephalina*. Finally, reweighting multistate characters resulted in a set of 10 MPTs of 305.2 steps. The consensus of these trees was very highly resolved, and differed from the tree shown in Figure 2.4 by lacking the same nodes as the unordered analysis. However, rather than being part of a large polytomy, *Elyx* is within a clade of *Bailiaspis* speces (as the sister group to node 11 of Fig. 2.4).

The poor resolution of the clade at node 9 in the main analysis, compared to in the first analysis, appears to be the result of different rooting when non-conocoryphids are included. The non-conocoryphid taxa, however, are intended only to suggest the broad relationships of the 'conocoryphid' clades recognized to sighted trilobites, and may not be very closely related to them. Complete resolution of the phylogenetic structure of this clade would require a comprehensive analysis of basal ptychoparioids to determine the most closely related taxa; this is clearly beyond the scope of this study.

Separate analyses including only the 24 taxa (coded for 39 informative characters) belonging to this clade (the emended Conocoryphidae, node 9 on Fig. 2.4) confirmed the importance of rooting. Fifty-five MPTs, 120 steps long, were found. The unrooted consensus of these trees supports only the *Bailiaspis-Tchaiaspis* (node 9 of Fig. 2.3, node 10 of Fig. 2.4), *Bailiella emarginata-Bailiaspis glabrata* (node 14 of Fig. 2.3) and *Ctenocephalus-Elyx* (node 18 of Fig. 2.3, node 13 of Fig. 2.4) clades. The topology of this group is therefore strongly dependent upon the position of the ancestral root. Analyses including the same set of 24 taxa and one of the two related non-conocoryphids for rooting (*Ptychoparia striata* and *Elrathia kingii*), produced very different topologies, as shown in Fig. 2.5. In view of these difficulties, systematic revision of the genera included in this clade (the emended family Conocoryphidae) is limited to those taxa that were supported by all of the analyses presented here. Further knowledge of the phylogeny of the 'generalised' ptychoparioids to which the restricted Conocoryphidae clade is related is required before its phylogeny can be established.

TAXONOMIC RANK AND MORPHOLOGICAL DISPARITY

Introduction and methods

The Ptychopariida is the most diverse Cambrian trilobite taxon. Biases and errors in the systematics of the group may therefore have had a profound effect on interpretations of patterns of evolution in trilobites during the early Palaeozoic. The diversity of higher taxa, such as families, has regularly been used as a proxy for other evolutionary metrics in palaeobiology (see e.g. Kemp 1999, pp. 157-158). There has been much recent discussion of the relationship between morphological diversity (hereafter referred to as disparity, see Wills *et al.* 1994) and taxonomic diversity during the Palaeozoic radiation. On the basis that disparity reached a maximum early in the Palaeozoic, it has been claimed that the rate of morphological diversification peaked earlier in the history of taxa than that of taxonomic diversification

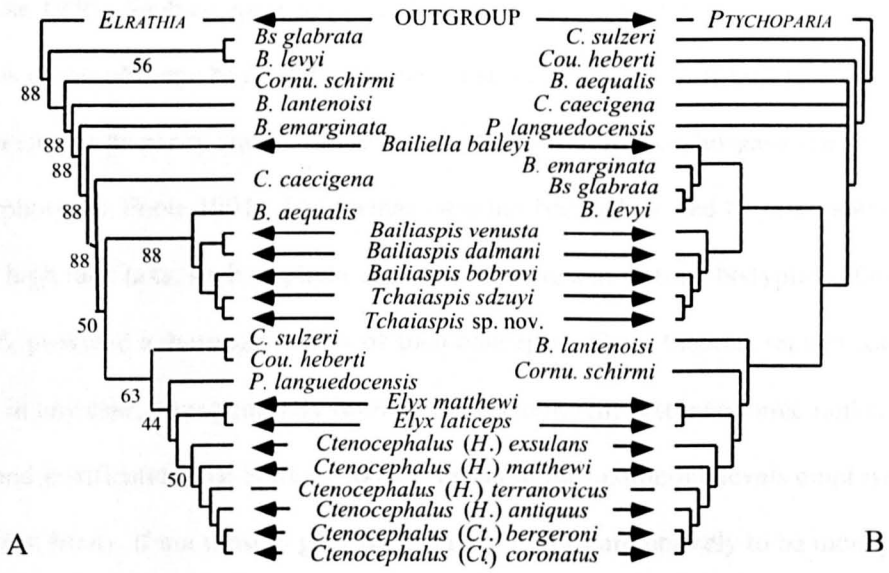


FIGURE 2.5. Consensus trees resulting from analyses of clade at node 9 (temended Conocoryphidae) of Figure 2.4, showing the effects of rooting on clade topology. A, majority-rule consensus of 32 MPTs 133 steps long (CI = 0.4286, RI = 0.6122) rooted using *Elrathia kingii*. B, strict consensus of 3 MPTs 126 steps long (CI = 0.4444, RI = 0.6296) rooted using *Ptychoparia striata*.

(Gould 1991; Foote 1993, 1999; Wagner 1995, 1997). Other studies have shown that disparity of arthropods may not have been significantly higher in the Cambrian than in the Recent (Briggs *et al.* 1992*a*, 1993), a result which may still suggest a rapid early increase in disparity. A number of possible explanations for such patterns have been suggested (e.g. Valentine 1986, 1995; Wagner 1996; Foote 1999).

Despite much interest in these problems, comparatively few studies have used morphometric approaches to study disparity; rather they have relied (in particular those with a wide taxonomic scope) on the use of higher taxonomic diversity as a proxy for disparity (Foote 1996). Such an approach would be valid if these taxa had some biological reality in terms of morphology beyond that of the constituent species, or if taxa of a particular rank had (1) a similar disparity and, (2) were evenly distributed in morphospace (i.e. represent morphotypes, Foote 1991). The former view has been advocated by some authors, who argue that high rank taxa, such as phyla and classes, represent distinct bodyplans (Gould 1991; Hall 1996, provided a thorough review of such concepts). These theories remain somewhat vague, but, in any case, have generally been restricted to the highest taxonomic ranks, so it is the second justification that is likely to be relevant at the taxonomic levels employed in most studies. Many, if not most, higher taxa in most groups are unlikely to be monophyletic (e.g. trilobite higher taxa analysed by Foote 1991; see Fortey 1990, 1997). Whilst this has no direct implications for their use as proxies for disparity, provided that the conditions outlined above are met, phylogenetic revision obviously leads to changes in taxonomy that may profoundly alter patterns based on such data. Interpretation of the results of studies in which probable non-monophyletic taxa are used may also be problematic (e.g. Foote 1991; Eble 1999).

The effect of using higher taxa as proxies for disparity, and the impact of subsequent taxonomic revision, were investigated by comparing the four blind trilobite clades identified herein with the polyphyletic Conocoryphidae previously recognized. Firstly, disparity was crudely measured as the mean number of character state differences within the sample, based on the matrix used for the cladistic analyses. Secondly, the taxa were ordinated onto principal coordinate (PCO) axes based on a matrix of intertaxon Euclidean distances (Wills *et al.* 1994).

The matrix of intertaxon distances was derived from the cladistic character matrix (Table 2) following the method of Wills *et al.* (*op. cit.*) for avoiding problems with negative eigenvalues. This allowed morphological disparity to be measured as ranges and variances for each of the samples, and the distance between the samples to be investigated. According to Kaiser's rule, the first eight PCO axes are significant. All analyses were carried out on the basis of the entire PCO space of 40 axes and, for comparison, on the first eight axes only. The relative merits of the many different possible disparity metrics have been discussed extensively (Foote 1999; Wills *et al.* 1994; see above). Rarefaction analysis was used to compare the expected disparity at different sample sizes, following the method of Foote (1992), using the computer application RARE 1.2 (Wills 1998), with 1000 bootstrap replicates at each sample size.

Results

The matrix of approximate Euclidean intertaxon distances, and the ordination onto 40 PCO axes derived from it are shown in Appendices 3 and 4, respectively. The results of the rarefaction analysis (Fig. 2.6, Table 3) indicate that the polyphyletic Conocoryphidae comprises considerably more disparity than the four clades identified herein. This does not depend upon the higher diversity of the total sample (40 taxa) than the sub-samples (3, 4, 9 and 24 taxa). In other words the four clades are far more cohesive morphologically than the polyphyletic group. All four samples fall well below the 95 per cent. confidence interval for disparity of the combined data, even at low sample sizes, as measured by the mean number of differing character states (Table 3A), or by the sum of ranges on the PCO axes (Table 3B-C). Similarly, morphological disparity appears to vary between the newly recognized clades. This result is however, somewhat equivocal, since it is sensitive to the method of assessing disparity. The Holocephalidae has the highest disparity of the four, in terms of character state differences or range on the first eight PCO axes, but a lower disparity than the emended Conocoryphidae when range on 40 PCO axes is used. The significance of differences

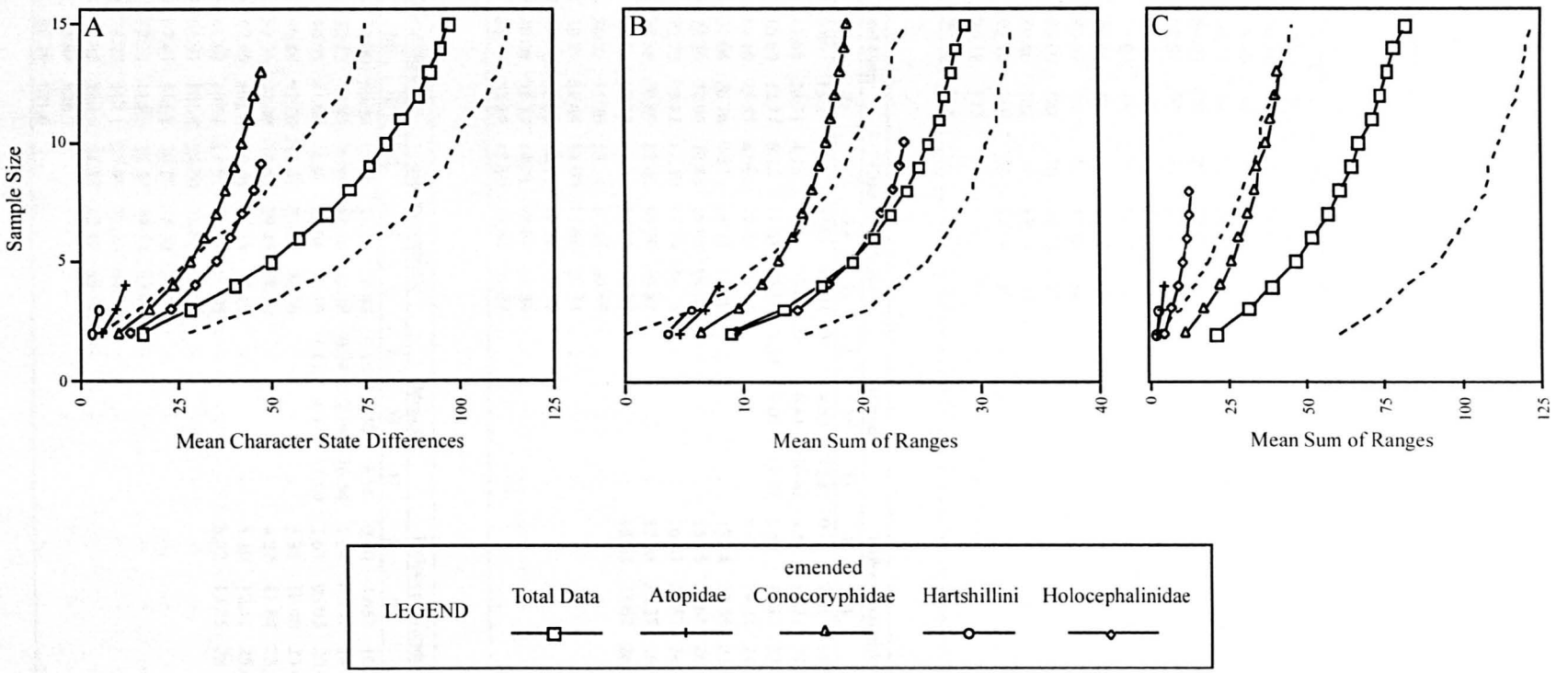


FIGURE 2.6. Results of rarefaction analysis of morphological disparity for all conocoryphidsa and the four monophyletic subgroups. A, measured as the mean number of character state differences. B, measured as the mean sum of rantges on the first 8 PCO axes, which are significant ccording to Kaiser's rule. C, measured as the mean sum of ranges on all 40 PCO axes. Dotted lines show the 95 per cent. confidence intervals of the disparity of the total data.

TABLE 3. Results of rarefaction analysis of morphological disparity, measured as (A) mean numbers of character state differences, (B) the sum of ranges on the first eight PCO axes and (C) the sum of ranges on all 40 PCO axes, for all 'conocoryphids' and the four monophyletic goups. Mean values (M) and 95 per cent. confidence limits (L = lower 95 per cent. confidence limit, U = upper 95 per cent. confidence limit) are shown, based on 1000 bootstrap replicates at each sample size.

A

	Total Data			Conocoryphidae			Atopidae			Holocephalinidae			Hartshillini		
N	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U
2	5	16.14	28	2	9.93	16	0	5.57	12	0	13.16	24	0	3.03	9
3	15	29.00	45	9	18.07	26	0	9.39	16	8	23.51	35	0	4.98	9
4	22	40.73	58	15	24.11	33	4	12.09	19	14	30.16	42	-	-	-
5	28	50.03	70	20	28.69	37	-	-	-	21	35.41	47	-	-	-
6	35	57.51	77	23	32.47	42	-	-	-	24	39.62	51	-	-	-
7	44	65.20	86	26	35.54	45	-	-	-	30	42.73	53	-	-	-
8	49	71.02	89	29	38.18	47	-	-	-	34	45.52	55	-	-	-
9	54	76.41	96	31	40.51	49	-	-	-	37	47.66	56	-	-	-
10	58	80.57	99	33	42.48	51	-	-	-	-	-	-	-	-	-
11	63	85.00	102	36	44.34	53	-	-	-	-	-	-	-	-	-
12	68	89.46	107	37	45.54	54	-	-	-	-	-	-	-	-	-
13	72	92.12	110	38	47.19	55	-	-	-	-	-	-	-	-	-
14	74	95.11	112	-	-	-	-	-	-	-	-	-	-	-	-
15	75	96.76	113	-	-	-	-	-	-	-	-	-	-	-	-

B

	Total Data			Conocoryphidae			Atopidae			Holocephalinidae			Hartshillini		
N	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U
2	0	9.09	15.21	0	6.30	11.04	0	4.58	7.65	0	9.41	16.64	0	3.67	7.87
3	6.15	13.66	20.31	4.15	9.53	13.81	0	6.81	10.61	4.51	14.71	21.95	0	5.59	8.46
4	9.18	16.60	22.77	6.12	11.53	15.80	3.52	8.02	11.01	6.54	17.17	23.89	-	-	-
5	11.48	19.10	25.37	8.09	12.92	16.96	-	-	-	8.97	19.21	24.91	-	-	-
6	14.26	21.06	26.76	9.87	14.22	17.90	-	-	-	13.74	20.55	25.55	-	-	-
7	15.52	22.33	27.96	10.83	15.02	18.65	-	-	-	15.15	21.61	26.10	-	-	-
8	17.27	23.77	29.12	11.30	15.78	19.30	-	-	-	16.37	22.57	26.38	-	-	-
9	18.39	24.88	29.89	12.01	16.39	19.82	-	-	-	17.65	23.27	26.62	-	-	-
10	19.27	25.56	30.38	13.01	17.03	20.32	-	-	-	18.63	23.62	26.75	-	-	-
11	20.22	26.52	31.30	13.34	17.45	20.57	-	-	-	-	-	-	-	-	-
12	21.50	26.99	31.45	14.00	17.80	20.74	-	-	-	-	-	-	-	-	-
13	22.39	27.62	32.05	14.21	18.26	20.98	-	-	-	-	-	-	-	-	-
14	22.65	28.08	32.33	14.91	18.62	21.34	-	-	-	-	-	-	-	-	-
15	23.80	28.78	32.59	15.19	18.84	21.29	-	-	-	-	-	-	-	-	-

C

	Total Data			Conocoryphidae			Atopidae			Holocephalinidae			Hartshillini		
N	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U
2	2.44	22.00	60.38	1.75	12.13	32.84	0.16	2.40	9.54	0.00	4.653	16.58	0.04	2.19	15.66
3	9.64	32.23	73.43	6.45	18.30	41.18	0.74	3.59	10.54	1.54	6.907	18.81	0.41	3.23	16.33
4	14.55	40.05	81.94	9.48	22.98	46.13	1.12	4.47	11.09	2.65	9.093	20.95	-	-	-
5	18.55	46.89	92.20	11.69	26.63	50.86	-	-	-	3.35	10.40	23.00	-	-	-
6	22.61	52.36	97.00	14.51	29.45	51.49	-	-	-	4.27	11.84	23.82	-	-	-
7	26.86	57.48	102.6	15.73	32.15	57.17	-	-	-	5.10	12.41	25.03	-	-	-
8	30.01	61.82	107.1	17.55	34.78	58.05	-	-	-	5.32	13.75	28.56	-	-	-
9	33.08	64.97	107.8	20.00	35.62	58.75	-	-	-	-	-	-	-	-	-
10	36.36	67.83	111.1	20.23	38.30	60.38	-	-	-	-	-	-	-	-	-
11	36.12	72.31	114.0	22.03	39.84	63.05	-	-	-	-	-	-	-	-	-
12	40.20	74.23	117.1	23.69	41.24	64.20	-	-	-	-	-	-	-	-	-
13	41.98	76.81	119.6	24.57	42.12	65.10	-	-	-	-	-	-	-	-	-
14	43.93	78.94	120.2	-	-	-	-	-	-	-	-	-	-	-	-
15	45.87	82.39	121.6	-	-	-	-	-	-	-	-	-	-	-	-

in disparity between the four taxa is difficult to assess because of the very low sample sizes of two of these taxa. The taxa considered clearly do not have a similar disparity. The first of the conditions outlined above for the use of taxa as proxies for disparity is therefore not met for suprageneric taxa of blind Cambrian trilobites, and is highly sensitive to phylogenetic revision of their taxonomy.

The distribution of the species in the first three dimensions of the PCO morphospace is shown in Figure 2.7 and their distribution in four dimensions in Figure 2.8. These dimensions represent 64 and 74 per cent. of the variance in the data, respectively (see Appendix 4). The four emended taxa clearly occupy different regions of morphospace, and do not appear to be evenly distributed within it. For example, the hartshillinid samples are closer to all of the atopids than they are to any of the conocoryphids. The distribution of the samples in morphospace was quantified by calculating the pairwise Euclidean distances between members of the four taxa. As shown in Table 4, there are large differences in the distances between the taxa. Non-parametric statistical tests (the Sign Test and Wilcoxon Signed Ranks Test, see e.g. Sokal and Rohlf, 1994) indicated that the differences between these distances are significant at the 95% confidence level in most cases. The difference in intertaxon distances between Hartshillini and Holocephalinidae and Hatshillini and Atopidae, Atopidae and Holocephalinidae and Hartshillini and Conocoryphidae were not significantly different, probably because of the small number of comparisons involved, and the difference between Atopidae-Holocephalinidae and Conocoryphidae-Holocephalinidae distances was not significant, because these distances are very similar. Thus the second condition required to allow taxonomic diversity to make a good proxy for disparity, that taxa are evenly distributed in morphospace, is also not met by these taxa.

If trilobite taxa in general are not a good proxy for disparity, the conclusions of any studies based on the trilobite taxonomic hierarchy may, at least in part, be an artefact of the recognition of non-monophyletic higher taxa. How closely taxa fit the requirements for their diversity to be an accurate estimate of disparity is likely to be extremely sensitive to their phylogenetic status, since more extensive taxonomic revision will be required in groups whose

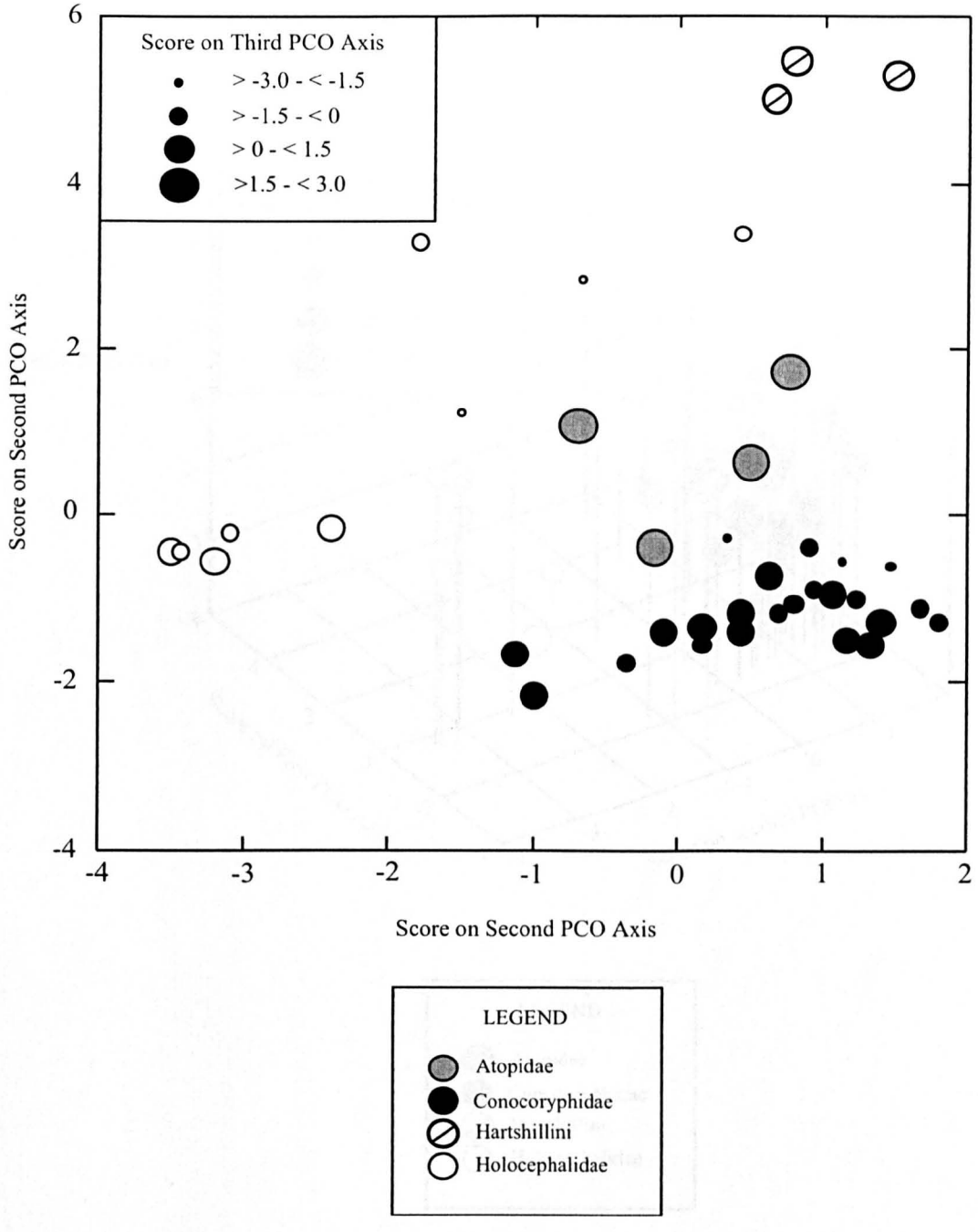


FIGURE 2.7 Distribution of conocoryphid taxa on the first three axes of the PCO morphospace. The first two PCO axes are shown as the axes of the graph and the third axis is indicated by the size of the circles.

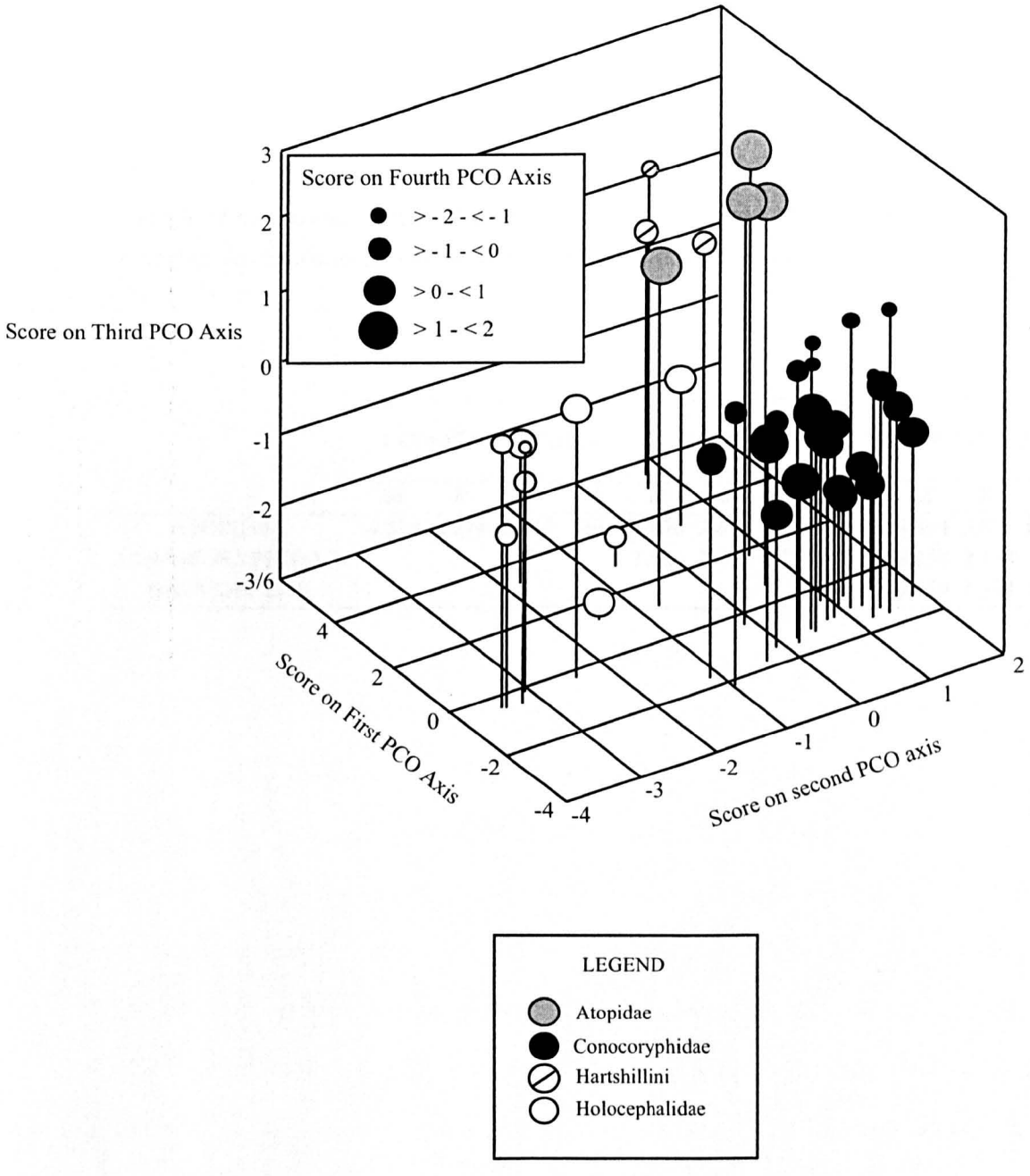


FIGURE 2.8. Distribution of conocoryphid taxa on the first four axes of the PCO morphospace. The first three PCO axes are shown as the axes of the graph and the fourth axis is indicated by the size of the circles.

TABLE 4. Mean pairwise intertaxon Euclidean distances (M), ranges (R) and variances (V) and number (N) of pairwise comparisons, between the four monophyletic suprageneric taxa recognised herein.

	CONOCORYPHIDAE				HARTSHILLINI				HOLOCEPHALINIDAE			
	M	R	V	N	M	R	V	N	M	R	V	N
ATOPIDAE	4.878	2.274	0.238	96	6.070	2.658	0.930	12	5.494	3.071	0.575	36
CONOCORYPHIDAE					7.026	2.461	0.285	72	5.258	3.138	0.412	216
HARTSHILLINI									6.319	4.344	2.088	27

taxonomy poorly reflects phylogeny. The use of taxonomic proxies for morphological disparity is likely to be unsafe when the phylogenetic status of the taxa used is uncertain.

DISCUSSION

Whilst the polyphyly of the Conocoryphidae has previously been suggested, it has not been convincingly demonstrated, and authors have differed widely in their hypotheses of relationships between the included genera. The cladistic analyses presented here clearly demonstrate the polyphyletic nature of the family Conocoryphidae Angelin, 1854, and suggest that four distantly related clades should be recognized in its place. Three of these clades are distributed amongst the basal ptychopariids, and the fourth consists of two genera assigned to the subfamily Acontheinae of the Corynexochida. These conclusions are robust to character sampling and assumptions about character evolution. The newly recognised families have wide geographic distributions, indicating their potential biostratigraphic utility. The Conocoryphacea have been characterized as one of the most secure of the superfamilies of the Ptychopariida. The wide taxonomic distribution of the clades previously included in the Conocoryphidae illustrates the potential degree of error inherent in traditional taxonomies, at least within the Trilobita. If this example were representative of the state of family level taxonomy in Cambrian trilobites as a whole, then any attempt to characterize evolutionary patterns in the Cambrian based on trilobite taxonomy is likely to involve overwhelming biases and errors. The high diversity of the Ptychopariida compared to other Cambrian trilobite groups suggests that, even if the taxonomic status of the Conocoryphidae is typical only of this order, significant biases may result.

The small number of other modern phylogenetic revisions of Cambrian trilobite taxonomy have found comparable levels of paraphyly and polyphyly in traditional classifications. The olenelloid family Laudoniidae and the suborder Olenellina were found to be paraphyletic, and the families Olenellidae and Holmiidae polyphyletic (compare Lieberman

1998 and Palmer and Repina 1993, 1997). Similarly, phylogenetic analyses of the Ptychagnostidae (Westrop *et al.* 1996) and Oryctocephalinae (Sundberg and McCollum 1997) have shown topologies strongly at odds with previous classifications. Westrop *et al.* (1996) quantitatively compare their results with previous classifications (e.g. Robison 1984*a*; Laurie 1988). They conclude that none of the genera recognized previously are monophyletic and reduce the family from around ten genera to only three. These studies suggest that the level of taxonomic error in the traditional classification of blind Cambrian ptychoparioids is representative of the situation in Cambrian trilobites as a whole.

Recognition of the repeated evolution of blindness in ptychopariids provides further evidence of the convergent nature of eye loss in trilobites (Fortey and Owens 1990; Clarkson 1997). The clades recognized here are all examples of the atheloptic morphotype, since their close relatives had normal eyes (Fortey and Owens 1987, 1990, 1997). It has previously been suggested that the mechanism of eye loss varied between members of one of the clades recognized here (the emended Conocoryphidae): '*Bailiella* has short, 'marooned' eye ridges and comparatively wide fixed cheeks, while *Conocoryphe* and *Meneviella* have long genal ridges and marginal sutures' (Fortey 1990, p. 563). Most species of *Bailiella*, however, have long eye ridges, with a very similar morphology to those of *Conocoryphe*. It is only in species such as *Bailiella emarginata* where the caecal system is not developed and only a single short ridge is present, rather than the two ridges (see above) of *Conocoryphe*, that the morphology differs (see Jell and Hughes, 1997, p. 62). There is therefore no evidence that the mechanism of eye loss in these genera was different, and following the cladistic results, blindness is considered here to be a valid synapomorphy of this clade.

A number of authors have suggested that levels of morphological variation in Cambrian trilobites were unusually high, and that this makes suprageneric classification difficult (McNamara 1986; Hughes 1991; Rushton and Hughes 1996). However, the suggested pervasive iterative evolution in Cambrian trilobites, and in ptychopariids in particular, has not been convincingly demonstrated. The level of homoplasy implied by a cladistic analysis of Cambrian trilobites has previously been suggested as evidence against this view (Lieberman

1998). The amount of homoplasy found in the analyses presented here (CI = 0.442 for the first analysis, CI = 0.342 for the second analysis) is slightly below average compared to other data sets of similar sizes (Archie 1989; Sanderson and Donoghue 1989), and far lower than that expected from random data (Klassen *et al.* 1991). Similarly, a recent cladistic analysis of alokistocarid phylogeny (Sundberg, 1999) found only moderate levels of homoplasy (19 taxa, 50 characters, CI = 0. 592). There is therefore no evidence that levels of homoplasy are unusually high in the Ptychopariida (*contra* Sundberg 1994), and no need to rely on a combination of stratigraphic data and overall similarity to form hypotheses about ptychopariid relationships. Resolution of ptychopariid phylogeny is likely to centre on the relationships of basal, generalized forms rather than more derived forms. Two of the groups recognised herein, the Holocephalidae and emended Conocoryphidae, consist of 'generalized' ptychoparioids. The recovery of highly resolved and well supported cladograms for such groups, both here and by Sundberg (1999), shows that cladistic methods have potential for resolving the problem of ptychopariid phylogeny, and that homoplasy is not so prevalent that such methods are of little use.

Many of the characters employed herein have not previously been regarded as phylogenetically significant, and are likely to be of more general use. A number of characters were of above average consistency (see Appendix 2 for a list of character consistency indices). These characters fall into easily recognized categories: nature of the cephalic borders, and shape of the cephalon, the form of the glabella, glabellar furrows and axial furrows, thoracic characters and gross morphology of the pygidium. Ptychoparioid trilobites show complex patterns of, often subtle, variation but there is no evidence that this variation is such that valid synapomorphies cannot be recognised, or that different sclerites show very different patterns of variation. Cladistic analysis provides a consistent approach to assessing the importance of variation in a wide range of characters, that other methods of phylogenetic reconstruction lack. Coding of detailed differences in morphology, and particularly in shape, should permit the resolution of the 'ptychoparioid problem' using cladistic methods.

SYSTEMATIC PALAEONTOLOGY

The taxonomy of suprafamilial taxa and previously recognized families follows the recent revision of the trilobite *Treatise of invertebrate paleontology* (Fortey 1997). Paraphyletic taxa are indicated using the quotes convention of Wiley (1979). The systematics of all family group taxa are dealt with in some detail and extensively revised, but a complete revision of all conocoryphid taxa at lower levels is beyond the scope of this work. However, the species-level systematics of members of the *Holocephalina-Holocephalites-Sdzuyella* clade (clade 30 of Figure 2.4) and genus-level systematics of the emended Conocoryphidae are discussed.

Class TRILOBITA *sensu* Ramsköld and Edgecombe, 1991

[see Edgecombe and Ramsköld, 1999]

Subclass LIBRISTOMA Fortey, 1990

Order 'PTYCHOPARIIDA' Swinnerton, 1915

Suborder 'PTYCHOPARIINA' Richter, 1932

[see Kaesler, 1997, p. 510, regarding authorship]

Superfamily 'ELLIPSOCEPHALOIDEA' Matthew, 1888

[see Nikolaisen and Henningsmoen 1990, p. 64, regarding authorship of this superfamily and of the 'Ptychoparioidea', below]

Family ATOPIDAE Hupé, 1953*c* emended herein

nom. corr. Cotton, 2001, p. 185 *ex* ATOPSIDAE Hupé, 1953*b*

Plate 1, figures 1-4, 8-9; Plate 2, figures 1-3.

Emended diagnosis. Blind ellipsocephaloid trilobites with thin 'threadlike' eye ridges that interrupt the axial furrows. Length of cephalon (sag.) less than 50 per cent. of cephalic width. Facial sutures only on cephalic border, librigenae consist only of a thin strip of the posterolateral border and genal spines on the dorsal surface. Anterior arch absent. Genal convexity moderate. Eye lobe absent. Threadlike genal ridges on external surface of anterior genae interrupt axial furrows adaxially, then run obliquely forwards before turning laterally and closely following the cephalic border furrow. Anterolateral cephalic border of even width, downsloping or weakly convex. Border furrow continuous across genal angles, posterior border furrow of even width or slightly expanding (exsag.) laterally. Caecal network present anterior to the genal ridges. Genal spines long (greater than 65 per cent. of sag. cephalic length) and directed backwards parallel to axis. Glabella prominent and convex (trans.), reaching or crossing anterior border furrow, at least 70 per cent. of cephalic length. Glabella sides approximately parallel to converging slightly forwards, especially anteriorly. Frontal lobe of glabella broadly rounded. Four pairs of straight or slightly curved lateral glabellar furrows usually visible, posteriormost pair may be transglabellar. Thorax consists of 17 or more segments. Pleurae with spinose terminations, macropleural spines may be present on some segments. Pleural furrows wide (exsag.), straight and transverse. Pygidium semicircular. Number of axial rings uncertain. Axis wide (trans.), reaching posterior border. Pleural furrows oblique, curved.

Included genera. Atops Emmons, 1844 (Pl. 1, figs 1-4) (= *Ivshiniellus* Korobov, 1966; Pl. 1, fig. 8); *Atopina* Korobov, 1966 (Pl. 1, fig. 9); *Pseudatops* Lake, 1940 (Pl. 2, figs 1-3).

Discussion. The members of this family show a number of similarities to the primitive libristomates, or advanced redlichiids, of the paraphyletic (see e.g. Fortey 1997) superfamily Ellipsocephaloidea. In particular, a number of features indicate a relationship with the Protolenidae (Protoleninae in the taxonomy of Geyer 1990): (1) the convexity of the cephalon and the definition of the furrows are distinct from the effacement of the Agraulidae and

EXPLANATION OF PLATE 1 (OVERLEAF)

Fig. 1. *Atops trilineatus* (Emmons, 1844). BMNH I.1587, Lower Cambrian, Washington County, New York; dorsal view; x 2·2.

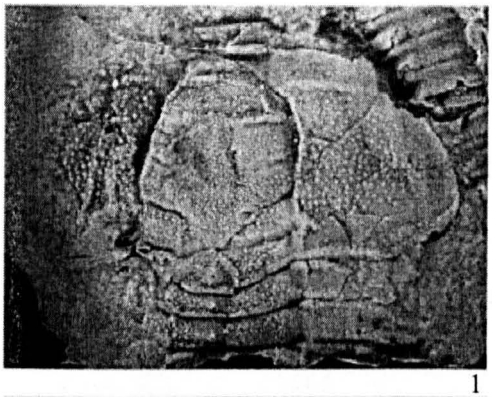
Figs 2-4. *Atops* sp. BMNH In.19186, Lower Cambrian, entrance to Saltwater Pond, Canada Bay, Newfoundland; 2, anterior view, 3, lateral view, 4, dorsal view; x 2·5.

Figs 5, 7. *Protolenus* (*Protolenus*) *elegans* Matthew, 1892. ROM 7795, syntype, Lower Cambrian, Hanford Brook, New Brunswick; 5, lateral view, 7, dorsal view; x 4·5.

Fig. 6. *Alacephalus contortus* Repina, 1960. CSGM 134/351, Lower Cambrian, Kuznetsky = Alatau, Russia; dorsal view; x 1·7.

Fig. 8. *Ivshiniellus nikolaii* Korobov, 1966. Cast of holotype GIN 91/3583, Lower Cambrian, Ezhim River, north Tuva, Russia; dorsal view; x 2.

Fig. 9. *Atopina antiqua* Korobov, 1966. GIN 89/3583, holotype, Lower Cambrian, Ezhim River, north Tuva, Russia; dorsal view; x 1·5.



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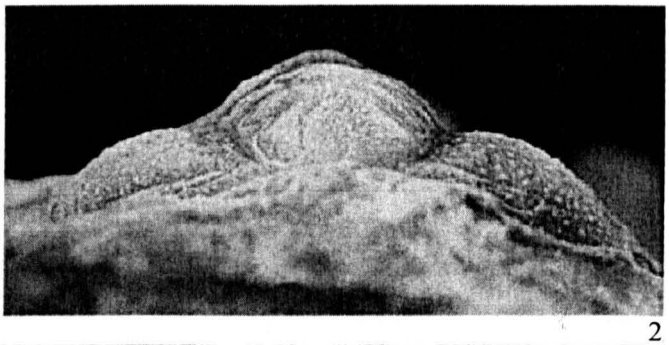

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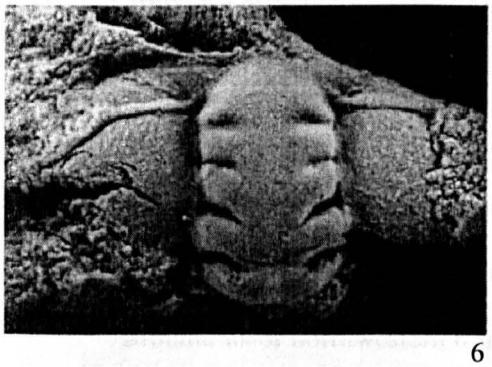

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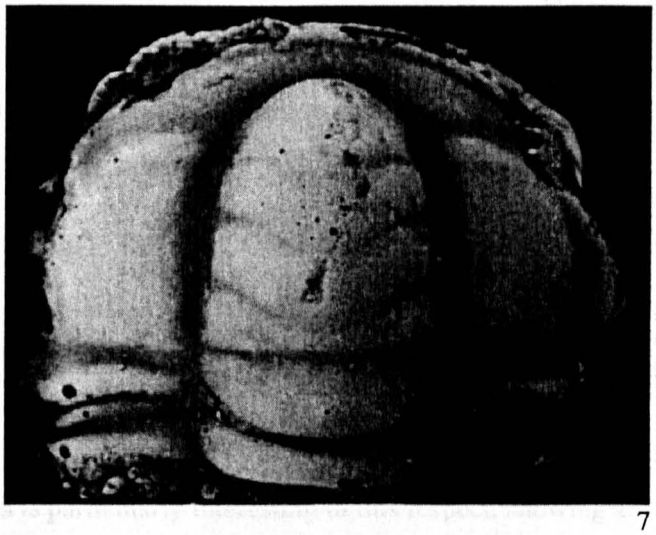

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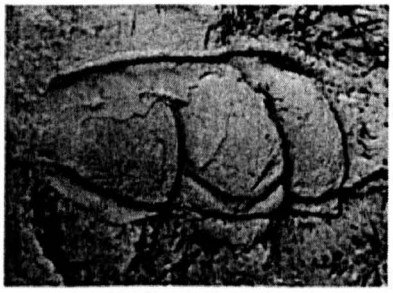

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Ellipsocephalidae; (2) the glabella of the protolenids is long and approximately parallel sided, compared to the shorter, tapering glabella of the ellipsocephalids. None of the ellipsocephaloids shows the distinctive form of the eye ridge, but some protolenids have eye ridges that are highly curved, positioned relatively far anteriorly, and directed relatively transversely, rather than obliquely posterolaterally (e.g. *Orodes schmitti* Geyer, 1990, pl. 51, figs 1-6; *Protolenus* (*Protolenus*) *elegans* Matthew, 1892; Pl. 1, figs 5, 7). In his emended diagnosis of the Protoleninae, Geyer (1990, p. 336) highlighted a number of characters that are found in the Atopidae, such as the long, convex glabella which is parallel sided posteriorly.

A few sighted Early Cambrian ptychoparioids show some resemblance to the atopids, and may be closely related. The genus *Rimouskia* has previously been compared to *Atops* (Richter and Richter 1941; Sdzuy 1961; Rasetti 1967) and is similar in the width of the fixigenae, the long, simple, subparallel lateral glabellar furrows, the shape of the glabella, and the form of the cephalic borders, but differs in the presence of eyes and the form of the eye ridge. A number of other Early Cambrian species share the long glabella and wide fixigenae. The three species of *Alacephalus*, *A. contortus* Repina, 1960 (Pl. 1, fig. 6), *A. latus* Repina and Romanenko, 1978, and *A*? *davisi* (see Lane and Rushton 1992, pl. 1; Blaker and Peel 1997, fig. 81), have a glabellar structure very similar to some species of atopid and to *Rimouskia*. *Gelasene acanthinos* Palmer (1968, pl. 2, figs 1-3, 5-6), from the Lower Cambrian of Alaska shares unusual double pleural spines with *Alacephalus*? *davisi*, but its long glabella is strongly tapered, the facial suture is complex and the genae relatively narrow (trans.). Fritz's conocoryphid sp. 1 (1973, pl. 6, figs 28-31), from the Lower Cambrian of the Mackenzie Mountains of northwestern Canada is particularly interesting in this respect, showing a combination of features that are typical of the Atopidae, including blindness, the form of the genal ridges, and the position of the suture, with a tapering glabella similar to that of *Gelasene, Nehanniaspis* Fritz, 1972 and *Keeleaspis* Fritz, 1972. In this species, the anterior pairs of lateral glabellar furrows are highly reduced compared to those in most other atopids and the posteriormost pair is transglabellar, both features shared with the unusual atopid *Atopina antiqua* Korobov, 1966. Fritz's species also shares a number of features with *Atops*?

calanus Richter and Richter, 1941 (also discussed by Sdzuy 1962), which, as previously argued (Orłowski 1985; Jell *et al.* 1992), should be excluded from the genus. Finally, these two species share some features with *Atops korobovi* Romaneko (*in* Repina *et al.*, 1999) and an undescribed species from Canada Bay, north-west Newfoundland (Pl. 1, figs 2-4), preliminarily assigned to *Atops*. Following the reasoning of Fortey (1990, p. 548), the absence of a preglabellar field in atopids and these other genera suggests that their affinities may lie with the conterminant ellipsocephaloids rather than the libristomate (= ptychopariid) ellipsocephaloids. This can only be confirmed when the ventral features are known. These unusual Lower Cambrian ptychoparioids are rather poorly documented, and a complete review is needed.

The interruption of the axial furrows by the eye ridges in atopids is likely to be homologous to the state in primitive ellipsocephaloids with eyes (Ahlberg and Bergström 1978). This character may be of diagnostic importance because, unlike the condition of hypostomal attachment, it is visible in the majority of material. If Fortey (1990) is correct, and the natant hypostomal condition originated somewhere within the Protolenidae, then the condition of the eye ridge at the axial furrows may define a clade within the Libristomata, excluding the protolenids and antatlasiids. The broad form of the pygidium in the Ellipsocephaloidea varies from typically redlichioid [e.g. *Palaeolenus antiquus* (Chernysheva), Rushton and Powell 1998, fig. 33] to ptychoparioid [e.g. *Kingaspis campbelli* (King), Rushton and Powell 1998, figs 22, 26], and pygidial morphology may provide a suite of useful characters, especially amongst effaced forms. The type material of the genus *Ivshiniellus* Korobov, 1966, is very poorly preserved, and it should not have been the basis of a new genus (Jell *et al.* 1992). The material is indistinguishable from *Atops*. Computer aided retrodeformation (see Jell and Hughes, 1997, pp. 17-18) of Korobov's (1966, 1973) illustrations of *Ivshiniellus* suggests that the greater forward tapering of the glabella is a preservational artefact. At least one of the species originally assigned to the genus, *I. nikolaii* (Korobov, 1966, pl. 6, figs 3-4), represents an atopid, on the basis of the form of the eye-ridges, the length of the glabella and the marginal position of the facial suture.

EXPLANATION OF PLATE 2 (OVERLEAF)

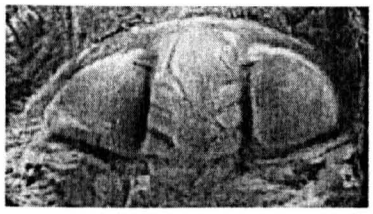
Figs 1-3. *Pseudatops reticulatus* (Walcott, 1890). BUGM 5961, Lower Cambrian, south of Comley Quarry, Church Stretton, Shropshire, cast of British Geological Survey Museum 53515; 1, dorsal view; x 1·4; 2, lateral view; x 2; 3, anterior view; x 1·4.

Figs 4-5. *Agraulos ceticephalus* (Barrande, 1846). Middle Cambrian, *Eccaparadoxides pusillus* zone, Skryje, Bohemia. 4, BMNH I.3434, dorsal view of almost complete exoskeleton; x 3·5. 5, BMNH 42368, dorsal view of cranidium; x 5.

Figs 6, 9-10. *Holocephalina primordialis* Salter, 1864. 6, BMNH 42648, holotype, Middle Cambrian, *Paradoxides davidis* zone, Porth-y-rhaw, St. Davids, Dyfed, Wales, dorsal view; x 6·5. 9-10 (ex *Holocephalina americana*), Middle Cambrian, Manuel's Brook Formation, Manuel's Brook, Newfoundland. 9, BMNH It.13584; x 4·3. 10, BMNH It.13585; x 3·5.

Figs 7-8. *Sdzuyella stremina* Hajrullina *in* Repina *et al.*, 1975. Holotype MMG 219/483, Turkestan Ridge, Uzbekistan; 7, dorsal view; x 3·8; 8, lateral view; x 4·5.

Fig. 11. *Holocephalites incertus* (Illing, 1916). Latex cast of NMW 80.34G.852, Middle Cambrian, *Tomagnostus fissus* zone, menevian beds, Penepleidiau, Caerfai Bay, St. Davids, Dyfed, Wales, dorsal view of almost complete exoskeleton; x 8·75



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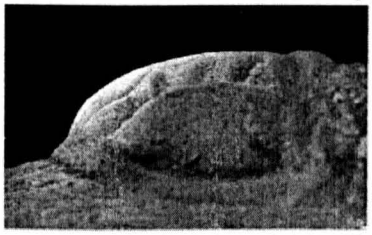

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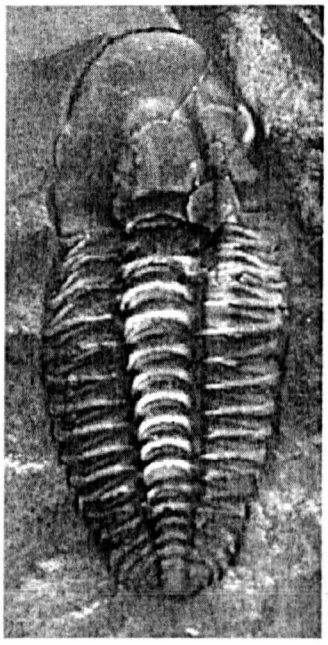

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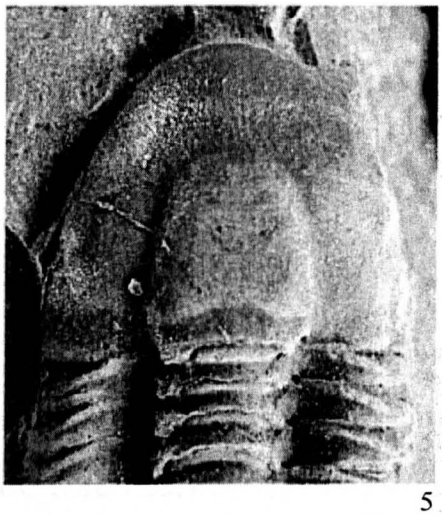

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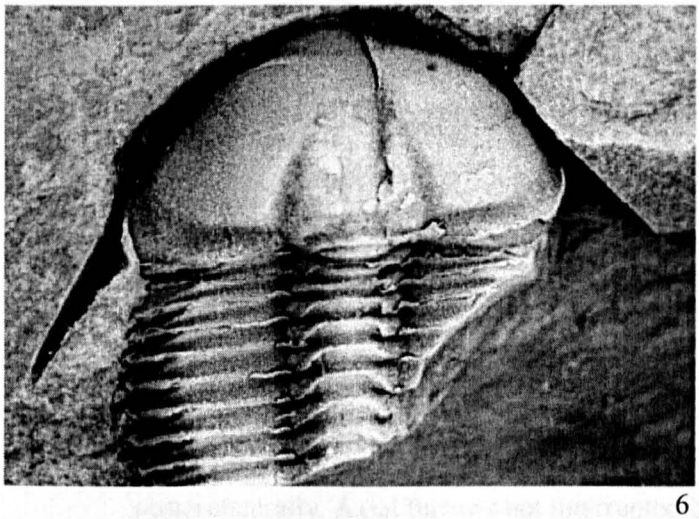

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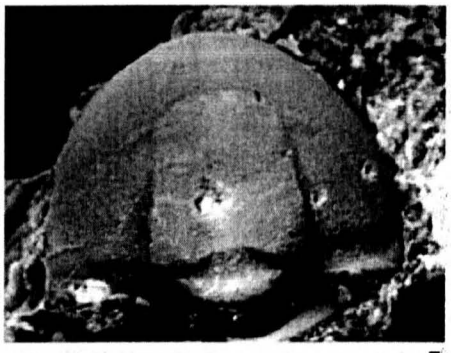

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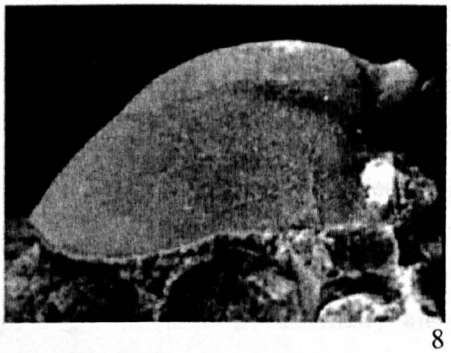

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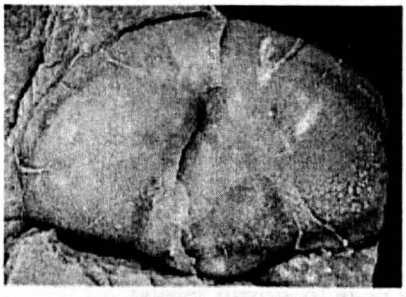

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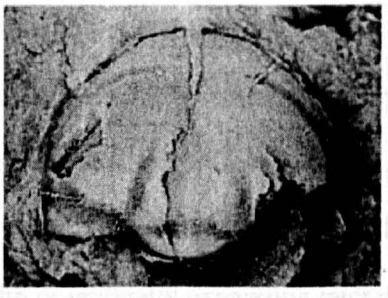

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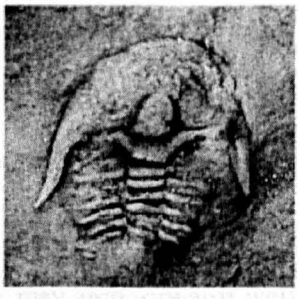

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Korobov's other species, *I. patulus,* is even more poorly preserved, and cannot be assigned to the family with confidence. Both species should be considered doubtful. The Australian species *Ivshiniellus briandailyi* Jenkins and Hasenohr, 1989, is referred to *Atops* herein. The tapering of the glabella in their reconstruction (fig. 4) is not matched by that of the specimens, and the species closely resembles the other Australian atopid, *Atops rupertensis* Jell *et al.*, 1992, in other respects.

Family HOLOCEPHALINIDAE Hupé, 1953*b* emended herein

nom. transl. Suvorova *in* Pokrovskaya, 1960 *ex* HOLOCEPHALINAE Hupé, 1953*b* [= HOLOCEPHALINAE Hupé, 1955; MENEVIELLINAE Hupé, 1955; HOLOCEPHALINIDAE Pokrovskaya, 1960; HOLOCEPHALINIDAE Egorova *et al.*, 1982; HOLOCEPHALIDAE Cotton, 2001]

Figure 2.2A; Plate 2, figures 6-11; Plate 3, figures 1-4.

Emended diagnosis. Blind agrauloid trilobites with short glabellae, dorsal librigenae consisting only of the genal spines, and downsloping genae. Cephalon wide in proportion to length, fixigenae very wide (facial sutures remain on cephalic border), consisting of thin strip of the border and the genal spine on dorsal surface. Palpebral lobes and eyes (visual surfaces) entirely absent. Preglabellar field wide (sag.), confluent with anterior genae, or slightly depressed relative to them. Prominent caecal network and genal ridges present, at least on internal moulds. Genal ridges very narrow (sag.), more or less straight and directed posterolaterally. Axial furrows not interrupted by eye ridge, which divides adaxially; anterior branches join around the front of the glabella, resulting in preglabellar furrow weaker than axial furrows. Prominent reticulate caeca posterior to the eye ridge. Anterolateral cephalic border moderately to entirely effaced or defined by broad, weak furrows, flat and sloping upwards or horizontal. Anterior border slightly wider axially than laterally. Posterior cephalic border furrow of even width or gradually expanding laterally, may arch forwards well inside genal angles, or become effaced at genal angles. Genal spines long and directed obliquely posterolaterally.

Glabella short to very short (sag., less than 0.6 cephalic length), tapering forwards. Three pairs of glabella furrows, variably defined. Thorax of 18 or more segments, terminating in short spines. Thoracic pleural furrows narrow, oblique and straight. Pygidium with short axis of three to four rings (excluding terminal piece). Wide postaxial field bearing furrows, pleural and interpleural furrows oblique and curved abaxially. Pygidium small, less than five per cent. of length of entire exoskeleton.

Included genera. Holocephalina Salter, 1864 (Pl. 2, figs 6, 9-10); *Dasometopus* Resser, 1936 (Pl. 3, fig. 5); *Holocephalites* Zhou *in* Zhou *et al.*, 1982 (Pl. 2, fig. 11); *Meneviella* Stubblefield, 1951 (Figure 2.2A; Pl. 3, figs 1-4) ; *Sdzuyella* Hajrullina *in* Repina *et al.*, 1975 (Pl. 2, figs 7-8).

Discussion. The correct name for this family is Holocephalinidae and not Holocephalidae, as previously suggested (Cotton, 2001, p. 190). At that time I was unaware that Suvorova (*in* Pokrovskaya, 1960) had corrected the stem from Hupé's (1953*b*) original name, and that consequently the incorrectly formed name cannot be considered to be in prevailing usage.

Two major groups of genera can be recognized within this family: (1) *Meneviella* and *Dasometopus*; (2) *Holocephalina*, *Holocephalites* and *Sdzuyella*. These groups may merit formal status when the phylogeny of basal ptychopariids becomes better known. Whilst superficially highly distinct, members of the two groups share a number of characters (see diagnosis above), and a close relationship is strongly supported by phylogenetic analysis. *Meneviella* and *Dasometopus* show few similarities to other groups, but the second group shares a number of characters with the Agraulidae. These include the short tapering glabella, flat genae, effaced anterior border furrow, and a long thorax. The pygidium is unknown from this second group, but that of *Meneviella* (Pl. 3, fig. 3) is similar in size and form to that of *Agraulos* (Pl. 2, fig. 4). The suprageneric classification of the Agraulidae and their putative relatives is unresolved; there is a great profusion of families and genera (see e.g. Zhang *et al.* 1980*b*; Zhang and Jell 1987). As with many effaced trilobite groups, few

EXPLANATION OF PLATE 3 (OVERLEAF)

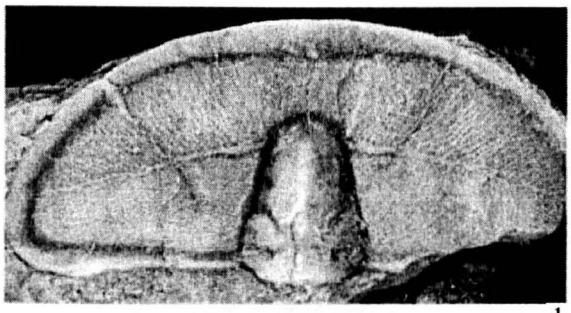
Figs 1-4. *Meneviella venulosa* (Hicks, 1872). 1, BMNH It.13575, Middle Cambrian, *Paradoxides davidis* Zone, Manuel's Brook Formation, Manuel's Brook, Newfoundland, dorsal view of cranidium; x 4. 2. BMNH 59319, Middle Cambrian, menevian beds; Porth-y-Rhaw, St. Davids, Dyfed, dorsal view of cephalon and anterior thoracic segments; x 2·25. 3, latex cast of BMNH I.7734, Middle Cambrian, near Dolgellau, Wales, pygidium; x 6. 4. BMNH I.7733, Middle Cambrian, near Dolgellau, Wales, dorsal view of cranidium and anterior thoracic segments; x 3.

Fig. 5. *Dasometopus* sp. Latex cast of NMW 80.34G.850, Middle Cambrian, *Hypagnostus parvifrons* Zone, menevian beds, St. Davids series, Porth-y-rhaw, St. Davids, Dyfed, distorted cranidium; x 6·5.

Figs 6, 9-10. *Conocoryphe sulzeri* (Schlotheim, 1823). 6, 9, BMNH 59826, Middle Cambrian, *Eccaparadoxides pusillus* Zone, Jince, Bohemia; 6, posterior thorax and pygidium; x 1·5; 9, cranidium and anterior thorax; x 1·8. 10, BMNH 42375, Middle Cambrian, *Eccaparadoxides pusillus* Zone, Ginetz, Bohemia, cranidium and anterior thorax; x 1·6.

Fig. 7. *Elrathia kingii* (Meek, 1870). BMNH It.20992, Middle Cambrian, Wheeler Shale, House Range, Utah, entire exoskeleton; x 2·75.

Figs 8, 11-12. *Ptychoparia striata* (Emmrich, 1839). 8,11, BMNH 42374, Middle Cambrian, Ginetz, Bohemia; 8, posterior thorax and pygidium, 11, cranidium; x 1·8. 12, BMNH I.3737, Middle Cambrian, Jince, Bohemia, cranidium; x 2.



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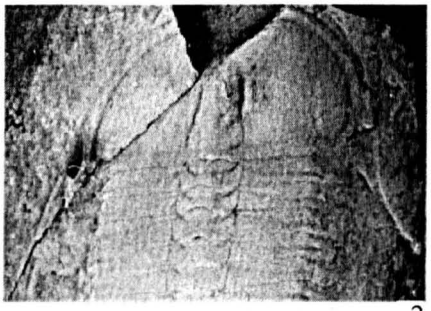

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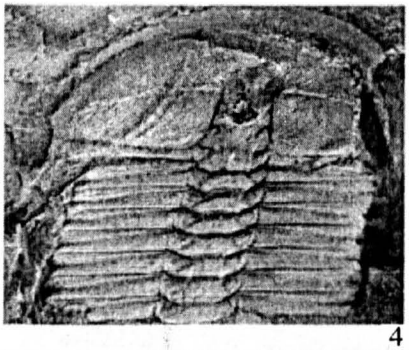

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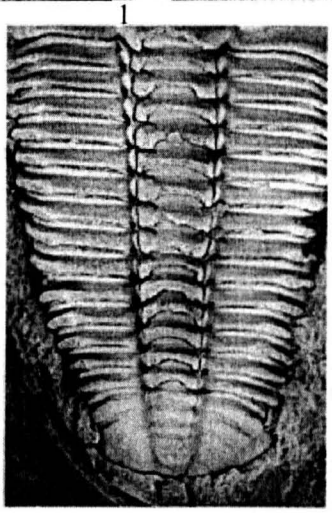

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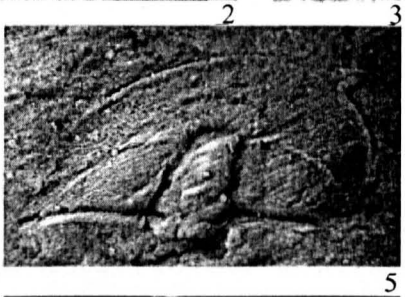

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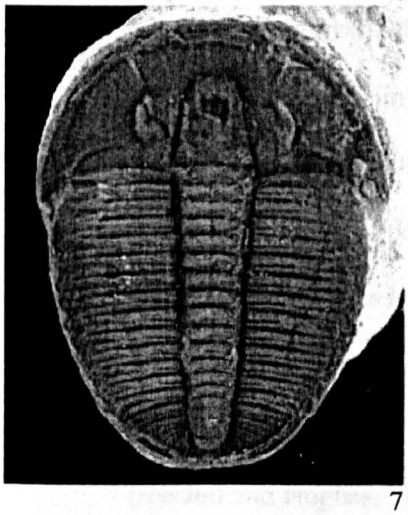

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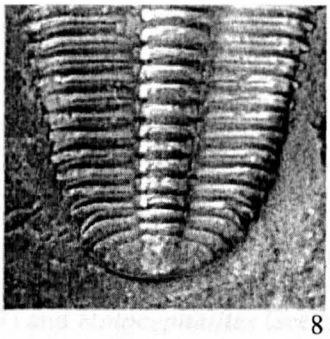

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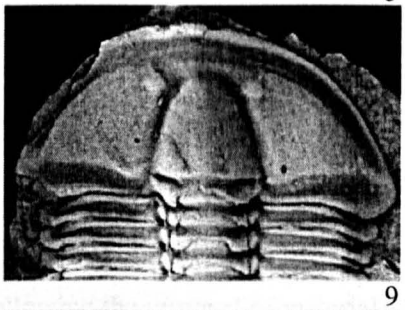

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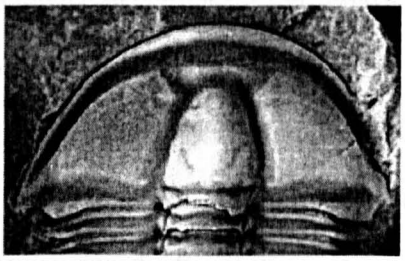

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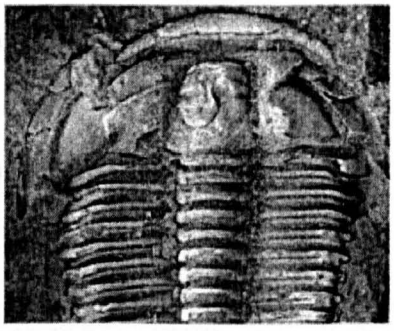

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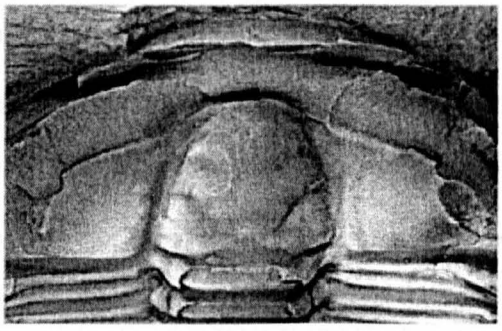

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characters are available to determine relationships between many of these taxa. Ahlberg and Bergström (1978) proposed that the agraulids are closely related to the ellipsocephaloids, and a number of authors have subsequently included them in the Ellipsocephaloidea (e.g. Geyer 1990; Fortey 1997). This approach is followed here.

Meneviella is unusually wide ranging geographically for Cambrian ptychoparioids, this may be because its distinctive morphology has enabled it to be consistently recognized throughout its range, in contrast to more generalized taxa (e.g. four generic synonyms of *Ptychoparella* Poulsen have been identified from Laurentia alone; Blaker and Peel 1997). Of the three described species, *M. venulosa* (Hicks, 1872) (see Morris 1988 for a discussion of the authorship of this species) has been described from Newfoundland, New York, England and Wales, Bornholm, Kazakhstan and eastern Siberia (reviewed by Lewis 1988), *M. viatrix* Shergold, 1973, is known only from Australia and *M. judomensis* Korobov (1973, p. 126, pl. 12, fig. 2) only from Siberia. Unidentified species of *Meneviella* have been reported from Lodochny on the Sisim River in eastern Sayan (Repina 1960, p. 222, pl. 17, fig. 11), and from the Olenek River, North Siberian Platform (Pokrovskaya 1965, p. 341).

Six nominal species remain in *Holocephalina* following the removal of material assigned to the genus by Miquel (1905; *Holocephalina holocephala*), Shah (1973; *Holocephalina wakhalooi*, *Holocephalina wadiai*) and Egorova *et al.* (1982; *Holocephalina* aff. *incerta*, *Holocephalina* sp.) to *Agraulos* (see Sdzuy, 1966; Courtessole, 1973), *Bailiella* (see Jell and Hughes, 1997) and *Holocephalites* (see below) respectively. Of these, *H. americana* Resser, 1937 (Pl. 2, figs 9-10), *H. menevenis* (Hicks 1872) and *H. teres* (Grönwall 1902) are probable synonyms of the type species following Lewis (1988, p. 286-287). The monophyly of the remaining species (*H. primordialis* (Salter, 1864, p. 237; Morris and Fortey, 1985, p. 74, pl. 1, fig. 6), *H. teres* Gozalo and Liñan (1996, p. 247, figs 1a-h) *and H. agrauloides* Sdzuy (1966, p. 75, pl. 9, figs 9-15; pl. 10, fig. 4) was not unambiguously supported by the cladistic analyses.

Holocephalina incerta Illing, 1916 was referred to the new genus *Holocephalites* Zhou *in* Zhou *et al.*, 1982 (type species *H. punctatus* Zhou *op. cit.*). The specimens of

Holocephalina described by Egorova *et al.* (1982, pl.3, fig. 14, pl. 9, fig. 11) as *Holocephalina* aff. *incerta* and *Holocephalina* sp. also belong within this genus. These specimens sharé a glabella that is extremely narrow (trans.) at the base compared to its length (sag.) and relatively strongly tapering forwards, and relatively deep (dorsoventrally) axial glabella furrows that expand (transversely) towards the base of the glabella. These features distinguish these specimens from other species of *Holocephalites*, and they are therefore likely to represent an undescribed *Holocephalites* species.

Superfamily 'PTYCHOPARIOIDEA' Matthew, 1888

Family CONOCORYPHIDAE Angelin, 1854 emended herein

Figure 2.2B; Plate 3, figures 6, 9-10; Plate 4, figures 1-11.

Emended diagnosis. Blind generalized ptychoparioids with anteriorly tapering glabella and convex genae. Fixigenae wide, position of facial suture variable. Anterior arch usually present. Cranidium approximately half as long (sag.) as wide (trans.), or slightly narrower (length between 0.45 and 0.65 of width). Preglabellar field may be separated from the genae by diverging preglabellar furrows, lowered relative to the anterior genae, or confluent with the cheeks. Genal spines directed backwards. Palpebral lobes usually absent. Threadlike genal ridges present, at least on internal moulds, rarely present on external surface, interrupted by axial furrows medially, run directly posterolaterally. Caecal network present on anterior genae on internal moulds only. Reticulate sculpture absent posterior to eye ridges. Threadlike ridges diverge to form a flattened subcircular boss just abaxial to the axial furrows. Cephalic border highly convex laterally, convex anteriorly but somewhat flattened where the border is expanded (sag.) anteromedially. Border defined by strong furrows both anteriorly and posteriorly, continuous across genal angles. Posterior border furrows of approximately even width along length, or widening halfway across genae, giving arched appearance.

Glabella tapering evenly over most of its length, anterior termination moderately rounded to blunt, usually of medium length (0.5-0.6 cephalic length) and narrow (0.25-0.31

EXPLANATION OF PLATE 4 (OVERLEAF)

Fig. 1. *Parabailiella languedocensis* Thoral, 1946. BMNH It.3964, Middle Cambrian, Coulouma, Hérault, France, cranidium; x 2.

Figs 2-3. *Bailiella baileyi* (Hartt *in* Dawson, 1868). Middle Cambrian, Fossil Brook Formation, Fossil Brook, St. Martins, New Brunswick, distorted cranidia. 2, BMNH It.3952; x 3. 3, BMNH It.3953; x 4.

Fig. 4. *Couloumania heberti* (Munier-Chalmas and Bergeron *in* Bergeron, 1889). BMNH 41892, Middle Cambrian, Coulouma, Hérault, France, cranidium; x 3.

Fig. 5. *Ctenocephalus* (*Ctenocephalus*) sp. BMNH I.2763. Middle Cambrian, Coulouma, Hérault, France, distorted cranidium; x 2.4.

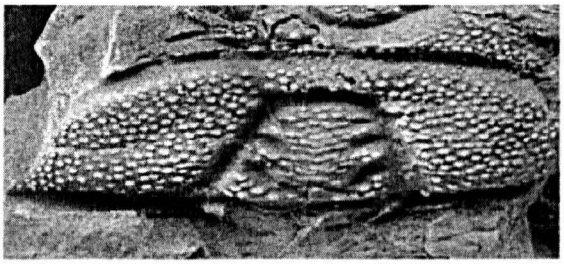
Fig. 6. *Elyx laticeps* (Angelin, 1851). BMNH It.2640. Middle Cambrian, *Paradoxides forschammeri* Zone, Andrarum Limestone; Andrarum, Scania, partly exfoliated ?cranidium; x 2·4.

Fig. 7. *Bailiaspis* (*'Bailiaspis'*) *venusta* Resser, 1937. NMW 88.55G.144, Middle Cambrian, *Paradoxides hicksi* Zone, Manuels River Formation, St. Davids Series, Manuels River, Avalon Peninsula, Newfoundland, cranidium; x 3.

Fig. 8. *Ctenocephalus* (*Ctenocephalus*) *coronatus* (Barrande, 1846). BMNH It.532. Middle Cambrian, Skryje, Bohemia, cranidium; x 3.

Fig. 9. *Bailiaspis* (*Tchaiaspis*) *sdzuyi* Korobov, 1966. Latex cast of holotype GIN 88/3583, Middle Cambrian, southern Siberian platform, Maya River, Chayskaya Hill, Siberia, Russia, ?cranidium; x 4.

Figs 10-11. *Ctenocephalus* (*'Hartella'*) *matthewi* (Hartt *in* Dawson, 1868). BMNH It.3930, Middle Cambrian, Fossil Brook Formation, Fossil Brook, St. Martins, New Brunswick; 10, cast of counterpart, 11, internal mould; x 4.



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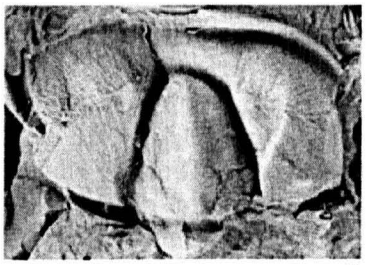

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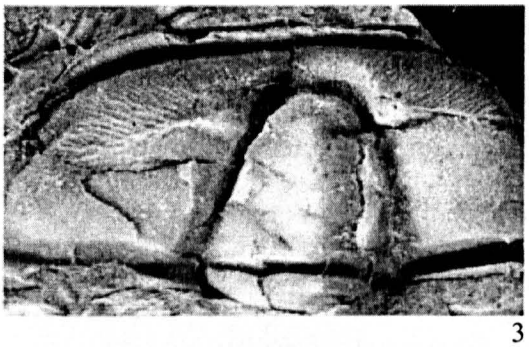

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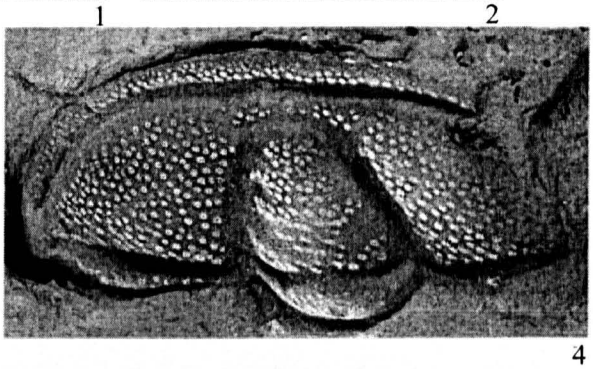

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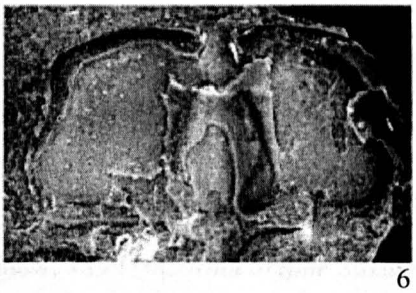

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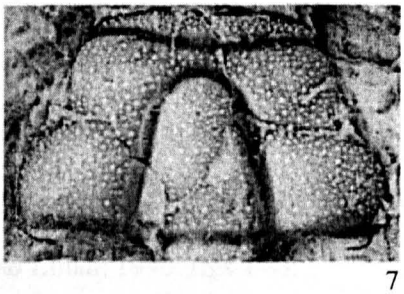

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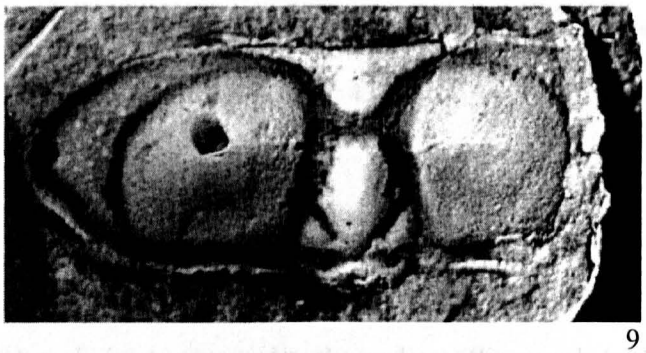

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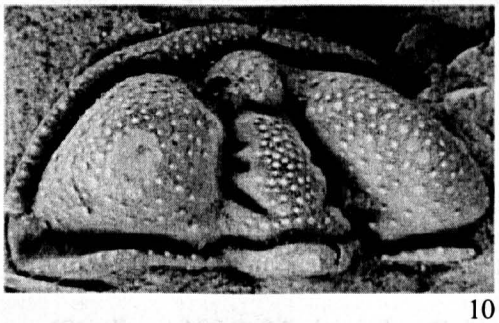

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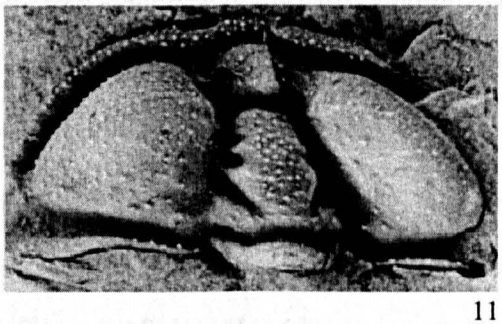

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cephalic width). Preglabellar furrow of similar definition to axial furrows. S1 lateral glabellar furrow simple (not bifurcating), may be recurved or simply curved. S2 furrows shorter than S1, longer than S3, oblique backwards. S3 furrows very short slits or indentations. Occipital ring of medium length. Paired prominent pits posterior to occipital furrow.

Thorax of 14 or 15 segments, with short, roundly pointed terminations with articulating facets. Thoracic pleural furrows wide, straight, and perpendicular to the axis. Axis of medium width (26-33 per cent. of thorax width). Pygidium of intermediate or large size, at least 6 per cent. of length of exoskeleton. Axis of four rings (excluding terminal piece), narrow postaxial field of approximately same width as pygidial border. Interpleural furrows absent, pleural furrows more or less straight, curving slightly posteriorly abaxially. Hypostome natant and of typical ptychoparioid morphology.

Included genera. Conocoryphe Hawle and Corda, 1847 (Pl. 3, figs 6, 9-10) (=*Couloumania* Thoral, 1946; Pl. 4, fig.4); *Bailiaspis* (*'Bailiaspis'*) Resser, 1936 (Pl. 4, fig. 7); *Bailiaspis* (*Tchaiaspis*) Korobov, 1966 (Pl. 4, fig. 9); *Bailiella* Matthew, 1885 (Figure 2.2B; Pl. 4, figs 2-3); *Cainatops* Matthew, 1899 (=*Cornucoryphe* Sdzuy and Liñan, 1996, figs 1-9); *Ctenocephalus* (*'Hartella'*) Matthew; 1885 (Pl. 4, figs 10-11); *Ctenocephalus* (*Ctenocephalus*) Hawle and Corda, 1847 (Pl. 4, figs 5,8); *Elyx* Angelin, 1854 (Pl. 4, fig. 6); *Parabailiella* Thoral, 1946 (Pl. 4, fig. 1).

Discussion. The Conocoryphidae, as emended here, is a clade of blind ptychopariids of otherwise 'generalized' (but nonetheless derived compared to the earliest ellipsocephaloid trilobites, see Geyer 1990) appearance. The sister group of the conocoryphids could lie amongst any of the sighted generalized ptychoparioids, a large number of family level taxa have been proposed for such forms, based on very few diagnostic differences. Such groups include the Antagmidae (Geyer and Malinky 1997), Dokimocephalidae, Ehmaniellidae (Sundberg 1994), Marjumiidae, Ptychopariidae, and Solenopleuridae, amongst others. These can hardly be differentially diagnosed, and the synonymy of many of these families has

frequently been suggested (e.g. Öpik 1967; Ahlberg and Bergström 1978, Fortey 1990; Blaker and Peel 1997), but rarely adopted. The use of another family name is defensible because the Conocoryphidae share the synapomorphy of blindness compared to these other generalized taxa, and can be readily distinguished from other blind trilobites by the characters described above.

The cladistic analyses presented herein provide little evidence for the monophyly of the largest conocoryphid genera, *Conocoryphe* Hawle and Corda, 1847 and *Bailiella* Matthew, 1885. The problem of defining these genera and the similar genera *Couloumania* Thoral, 1946 and *Parabailiella* Thoral, 1946 remains. Distinction between these four taxa currently rests on two features (Westergård 1950; Courtessole 1973; Jell and Hughes 1997): (1) the position of the facial suture with respect to the border furrow (on the border in *Conocoryphe* and *Coulomania,* crossing it in *Bailiella* and *Parabailiella*), and (2) the possession of diverging preglabellar furrows (present in *Conocoryphe* and *Parabailiella*, absent in *Bailiella* and *Couloumania*). The analyses presented here indicate that the first is the more important; it has a higher character consistency index on all the cladograms. This is supported by the phylogenetic position of the species *Bailiella lantenoisi* (Mansuy, 1916), in which the preglabellar furrows are absent, but the sutures remain on the border (see Jell and Hughes 1997). This species and *Bailiella aequalis* consistently fall outside the *Bailiella* clade in the cladistic analysis, and the generic assignment of both of these species has previously been questioned. Resser (1936, p. 15) suggested that a new genus may be necessary for *B. lantenoisi*, and Courtessole (1973, pp. 195-197) compared *Bailiella aequalis* to *Parabailiella.*

When proposing the genus *Tangshihella* (misspelt *Tangshiella* in Harrington *et al.*, 1959, p. O242 and subsequently), with the type species *Bailiella ulrichi* Resser and Endo, 1937 (p. 193), Hupé (1953*c*) made no attempt to differentiate the taxon from any other. Therefore, according to Article 13 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999), this name is not available. *Bailiella ulrichi* and *Liaotungia puteata* Resser and Endo *in* Kobayashi, 1935 (p. 89, pl. 24, fig. 15), the type species of *Liaotungia*, are junior synonyms of *Bailiella lantenoisi* (see

Zhang and Jell, 1987, p. 80-81). When the phylogeny of *Bailiella* is better understood, a new genus or subgenus may be necessary for this species for which the name *Liaotungia* is available.

The species *Conocoryphe caecigena* Dean, 1982, is representative of a group of six very similar species (reviewed by Dean *op. cit.*) in the cladistic analyses, all previously assigned to *Conocoryphe*. They do not share the essential features of *Conocoryphe*, being more similar to *Couloumania* in that the suture remains on the border and the diverging preglabellar furrows are absent. They also have the unique (within the Conocoryphidae clade) synapomorphy of pseudoculate (see Courtessole 1973; Dean 1982) protuberances on the genae, which are likely to represent non-functional homologues of the palpebral lobes. They do not appear to be closely related to *Conocoryphe*, and a new genus should be erected to accommodate them. The type species of *Couloumania*, *C. heberti*, appears to be closely related to *Conocoryphe sulzeri*, and *Couloumania* is therefore considered to be a subjective junior synonym of *Conocoryphe*.

Tchaiaspis Korobov, 1966 clearly shares a number of derived characters with *Bailiaspis* and was nested within a clade of *Bailiaspis* species (including *B. dalmani*, a probable senior synonym of the type species *B. elegans* Hartt *in* Dawson, 1868, p. 650, according to Lewis 1988) in all cladistic analyses performed. Korobov (1973, p. 144) himself recognised that *Tchaiaspis* was derived from within *Bailiaspis*. In order to avoid rendering the genus *Bailiaspis* paraphyletic, *Tchaiaspis* is here regarded as a subgenus of *Bailiaspis*. A second species of *Tchaiaspis* has been described in open nomenclature (Egorova *et al.* 1982) and figured by St. John and Babcock (1997). It has been described by in an unpublished thesis (St. John 1994), and will shortly be formally erected by St. John and Babcock. The analyses provide strong evidence that *Bailiaspis glabrata* (Angelin 1854) should be assigned to the genus *Bailiella*, as tentatively suggested by Sdzuy (1966); it was included in a clade of *Bailiella* species in all analyses.

The synonymy of *Cainatops* and *Cornucoryphe* is tentatively suggested. *Conocoryphe pustulosa* Matthew (1897, p. 174) is extremely poorly known, and has only been illustrated by

drawings of a single cephalon (Matthew, *op. cit.*, pl. 1, figs 8a-b). This illustration and Matthew's description, however show no characters that differ significantly from *Cornucoryphe schirmi* Sdzuy and Liñan, 1996, and the shared possession of a cephalic border spine is suggestive of a relationship between these species. Matthew's specimens are probably in the collections of the Royal Ontario Museum, Toronto, according to Resser (1937, p. 16).

Order CORYNEXOCHIDA Kobayashi, 1935

Suborder CORYNEXOCHINA Kobayashi, 1935

Family CORYNEXOCHIDAE Angelin, 1854

Subfamily ACONTHEINAE Westergård, 1950, emended Geyer, 1994

[=TRINIIDAE Poletaeva, 1956, p. 17; TRINIINAE Suvorova, 1964, p. 227; CORYNEXOCHELLINAE Suvorova, 1964, p. 229; ABAKANIINAE Romanenko *in* Repina *et al.*, 1999, p. 17]

Discussion. Geyer (1994) extensively discussed this subfamily, and his concept of the subfamily is adopted here. Repina *et al.* (1999) reject Geyer's revision and base their classification on the presence or absence of eyes and facial sutures, uniting sighted forms in the family Milaspidae. As demonstrated here, and discussed above, blindness is of little phylogenetic significance in trilobites, and Geyer's arguments for a close phylogenetic relationship between proparian and blind corynexochoids is accepted.

Three subfamilies, Abakaniinae, Milaspinae and Triniinae, were included in the Milaspidae by Repina *et al.* (1999). The Triniinae was included in the Acontheinae by Geyer (1994). The subfamily Abakaniinae Romanenko (*in* Repina *et al.* 1999) also fits Geyer's concept, and is synonymized with the Acontheinae herein. *Milaspis* (*see* Repina *et al.*, 1999, pp. 17-19, pl. 2, figs 2-9), the only genus in the Milaspinae, differs from the other trilobites discussed here in a number of respects, including relatively wide and flat fixigenae and wide and spinose thoracic pleurae, and is excluded from the Acontheinae.

Tribe HARTSHILLINI nov.

Diagnosis. Blind and strongly effaced corynexochids with anteriorly expanding glabella and distinctive punctate sculpture. Cephalon very narrow compared to length (length greater than 75 per cent. of cephalic width), long in proportion to entire exoskeleton (greater than 40 per cent. of total length). Facial suture entirely absent on dorsal surface. Blind; palpebral lobes, visual surfaces and genal ridges all absent. Lateral glabellar furrows and anterolateral cephalic border entirely effaced. Posterior cephalic border entirely effaced or indicated by lack of punctate sculpture on exterior surface, becomes entirely effaced at genal angles. Prominent, punctate cephalic sculpture (granulose on internal casts) may be missing from posterior cephalic furrows.

Anterior glabella, genae and border confluent. Glabella long and expanding (trans.) anteriorly, clavate, may be slightly raised above genae or confluent with them (especially in holaspids). Axial furrows weakly expressed near occipital furrow, completely effaced, or represented by impunctate bands. Occipital furrow entirely effaced or indicated by smooth bands. Occipital ring extended into long spine or short rounded protuberance.

Thorax of eight segments, with blunt, facetted terminations, and a wide axis (greater than a third of total thoracic width). Thoracic pleural furrows narrow, oblique and highly curved. Pygidium at least 10 per cent. of length of entire exoskeleton. Axis of two rings and terminal piece, width at least 35 per cent. of maximum pygidial width (both trans.), without postaxial field. Hypostome conterminant and fused to rostral plate.

Included genera. Hartshillia Illing, 1916; *Hartshillina* Lake, 1940.

Discussion. The tribe Hartshillini is erected within the Acontheinae to accommodate the highly derived genera *Hartshillia* and *Hartshillina*. These genera are most similar to blind *Acontheus* species, such as *Acontheus acutangulus* Angelin (Westergård 1950, p. 9, pl. 18, figs 4-6) and *Acontheus burkeanus* Öpik, 1961*b*, sharing a similar shape of the glabella, the

position of the facial suture and a distinctive punctate sculpture. *Hartshillina* shares some distinctive characteristics of the pygidium with other members of the Acontheinae (see Geyer 1994), and is generally less effaced than *Hartshillia*, and so is likely to be the sister taxon to *Hartshillia*. Considering the degree of variation, particularly in characters relating to effacement, amongst specimens assigned to *Hartshillia inflata* (Hicks, 1872) from Britain (Lake 1938) and Greenland (Babcock 1994*a*), the validity of the other species assigned to the genus: *H. clivosa*, *H. pusilla* and *H. taimyrica*, all Lazarenko, 1965, and *H. terranovica* Hutchinson, 1962, is in need of reassessment. The Hartshillini will be discussed in more detail elsewhere.

3. THE PHYLOGENY OF ARACHNOMORPH ARTHROPODS: BODY-PLAN EVOLUTION AND THE ORIGINS OF THE CHELICERATA

THE phylogeny of arthropods has been the subject of heated debate for over a century. Whilst five major groups, the extant Chelicerata, Hexapoda, Crustacea and Myriapoda and the extinct Palaeozoic Trilobita, have more or less consistently been recognised the relationships between these groups have been highly contentious (see Wheeler *et al.* 1993; Wills *et al.* 1995). Recently, however, some consensus has been reached on issues such as the monophyly of the euarthropods and the sister-group relationship between crustaceans and hexapods, forming the Mandibulata (Budd 1996*a*; Akam 2000). Furthermore, all recent cladistic studies that have included fossil taxa have recognised trilobites and chelicerates as more closely related to each other than either group is to mandibulates (see e.g. Ax 1986; Bergström 1992; Weygoldt 1998; Wills *et al.* 1998*a*). This clade has variously been given the names Arachnomorpha (Størmer 1944; 1951; Briggs and Fortey 1989; Briggs *et al.* 1992*a*; Wills *et al.* 1995; Weygoldt 1998), Lamellipedia (Hou and Bergström 1997) or Arachnata (Lauterbach 1973, 1980, 1983; Chen *et al.* 1997; Ramsköld *et al.* 1997; Edgecombe and Ramsköld 1999; although Lauterbach apparently later rejected the term Arachnata and included all the assigned taxa in the Chelicerata, see Müller and Walossek, 1987, p. 53). The latter term has recently been most extensively used, but the current concept of the group is closer to that of Størmer than of Lauterbach and the earlier name Arachnomorpha (originally proposed by Heider in 1913) is therefore used herein. This group can be defined as the most inclusive clade including Chelicerata but not Crustacea (following Chen *et al.* 1997; Ramsköld *et al.* 1997). According to this definition the Arachnomorpha consists of the chelicerates and their stem-group (*sensu* Ax 1986), as illustrated by Figure 3.1. Therefore resolving arachnomorph phylogeny may have important implications for our understanding of chelicerate evolution (see Dunlop, 1999).

In addition to the Trilobita and Chelicerata, Størmer (1944) included in his Arachnomorpha a seemingly highly disparate (Gould 1989, 1991) assemblage of Palaeozoic fossil arthropods, the Trilobitomorpha (Størmer 1944) or Trilobitoidea (Størmer 1959). These included various problematic arthropods from the famous Middle Cambrian Burgess Shale of British Columbia, Canada (see Conway Morris 1982; Briggs *et al.* 1994) and *Cheloniellon* and *Mimetaster* from the Devonian Hunsrück Slate of Germany (see Bartels *et al.* 1998). Since then, our knowledge of arachnomorph diversity has been transformed by the discovery of many new taxa from Cambrian Burgess-Shale type faunas and to a lesser extent later faunas from around the world. Of primary importance amongst these new Lagerstätten (reviewed by Conway Morris 1989) is the Chengjiang fauna from the Lower Cambrian of Yunnan, China (see Hou *et al.* 1991; Chen *et al.* 1996; Hou and Bergström 1997).

These new finds consist largely of taxa similar to, and have consequently improved our knowledge of, those from the Burgess Shale. For example, the Chengjiang fauna includes taxa that are clearly closely related to each of *Helmetia* Walcott, 1918, *Tegopelte* Simonetta and Delle Cave, 1975 and *Alalcomenaeus* Simonetta, 1970 (Edgecombe and Ramsköld 1999). Similarly the most widespread trilobitomorph group, the Naraoiidae (*sensu* Fortey and Theron 1994) or Nektaspida (*sensu* Hou and Bergström 1997), was originally known only in the form of *Naraoia* Walcott, 1912*b* from the Burgess Shale. A number of related genera are now recognised from the Early Cambrian of Poland (*Liwia* Dzik and Lendzion, 1988), China (*Misszhouia* Chen *et al.*, 1997) and Greenland (*Buenaspis* Budd, 1999*a*), and the Ordovician of Sardinia (*Taricciola* Hammann *et al.*, 1990) and South Africa (*Soomaspis* Fortey and Theron, 1994). *Naraoia* itself has now also been described from the Early Cambrian of Idaho, the Middle Cambrian of Utah (both Robison 1984*b*) and from the Chengjiang fauna (Zhang and Hou 1985). However, some of the probable arachnomorphs from Cambrian exceptionally-preserved faunas have no obvious affinities to others, despite detailed knowledge of their morphology. Notable among these are *Emeraldella* Walcott, 1912*b* and *Sidneyia* Walcott, 1911 from the Burgess Shale, *Retifacies* Hou *et al.*, 1989

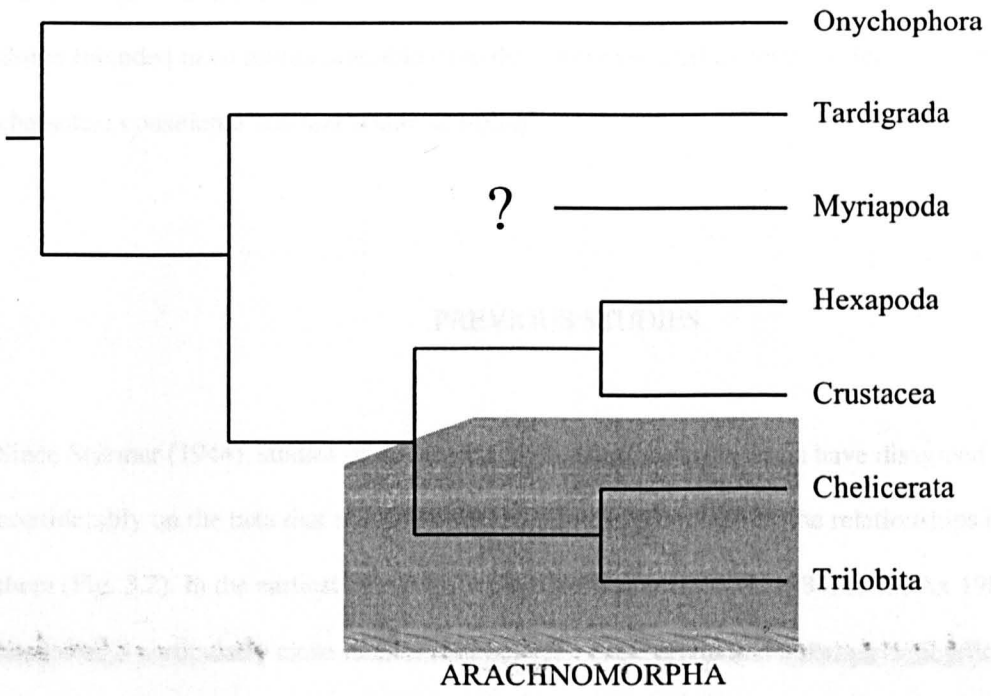


FIGURE 3.1. Widely accepted relationships between major arthropod groups, illustrating the Arachnomorpha concept proposed by Chen *et al.* (1997) and followed here.

from the Chengjiang fauna and *Phytophilaspis* Ivantsov, 1999 from the Lower Cambrian Sinsk Formation of Siberia. Other taxa are enigmatic because they are poorly known.

Despite uniformally supporting an arachnomorph clade including the trilobites and various Cambrian trilobite-like or merostome-like arthropods, recent studies have largely failed to provide convincing synapomorphies for the group (Dunlop 1999). Here cladistic methods are used to address this problem, to rigorously assess the limits of the Arachnomorpha, and to determine relationships within the arachnomorph group as a whole. This study is based upon a new matrix that is intended to be more comprehensive than previous work in terms of both the range of characters considered and taxonomic sampling.

PREVIOUS STUDIES

Since Størmer (1944), studies of the phylogeny of the Arachnomorpha have disagreed considerably on the taxa that should be included in the group and on the relationships between them (Fig. 3.2). In the earliest relevant cladistic study, Lauterbach (1980, 1983; Ax 1986) suggested a particularly close relationship between chelicerates and a paraphyletic trilobite group, an hypothesis originally proposed by Raw (1957). They argued that olenellid trilobites (see Palmer and Repina 1993, for a review) were the sister-group to chelicerates and other trilobites were the sister-group to this clade. This idea has been extensively criticised. In particular, Lauterbach (1980, 1983) ignored all other arachnomorph taxa (including more plesiomorphic trilobites) and a wide range of characters that are potential trilobite synapomorphies (Fortey and Whittington 1989; Fortey 1990*a*; Ramsköld and Edgecombe 1991; Bergström and Hou 1998). To our knowledge, no subsequent author except Weygoldt (1998) has accepted Lauterbach's hypothesis.

Most hypotheses of arachnomorph phylogeny have been presented as part of analyses of the phylogeny of arthropods as a whole. The pioneering cladistic work of Briggs and Fortey (1989,

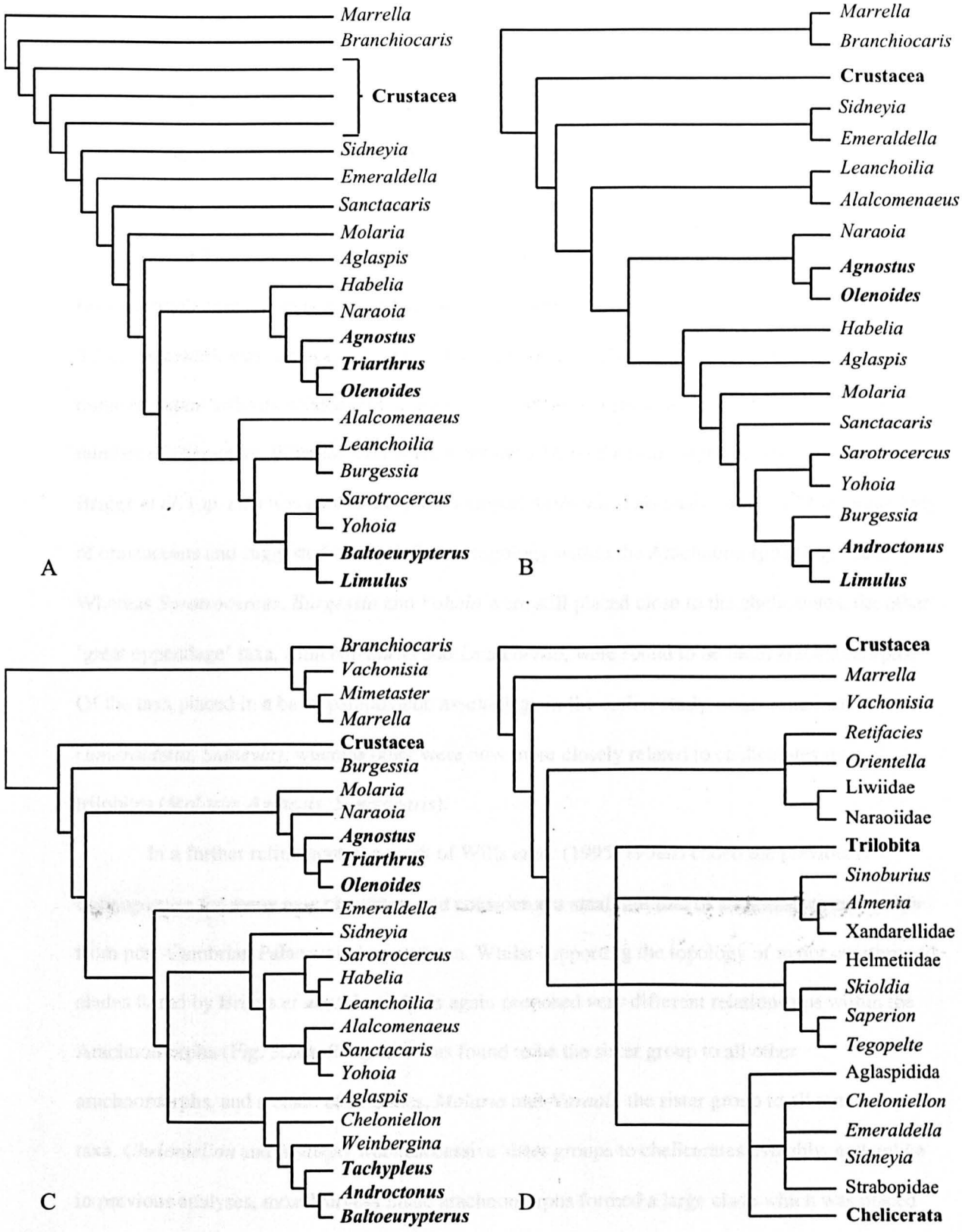


FIGURE 3.2. Previous hypotheses of arachnomorph phylogeny. A. after Briggs and Fortey (1989, fig. 1; 1992, fig. 3), note that the Crustacea were found to be paraphyletic in this analysis. B. after Briggs *et al.* (1992, fig. 3; 1993, fig. 1). C. after Wills *et al.* (1995, fig. 1A; 1998*a*, fig. 2.1). D. after Hou and Bergström (1997, fig. 88), for monotypic families, the family names of monotypic families used by Hou and Bergström have been replaced with generic names. Taxa important for the recognition of an arachnomorph clade (trilobites, chelicerates and crustaceans) are shown in bold type.

1992) found that the crustaceans (and Cambrian 'crustaceanomorphs') were paraphyletic with respect to arachnomorphs. Within the arachnomorphs a strongly pectinate paraphyletic group including *Aglaspis* and various Burgess Shale arthropods was primitive with respect to a clade of all other taxa. This consisted of a (*Habelia* (*Naraoia*, Trilobita)) group and a clade including the Burgess Shale 'great appendage' arthropods, *Burgessia*, *Sarotrocercus* and chelicerates (Fig. 3.2A). This work was subsequently revised (Briggs *et al.* 1992*a*, 1993) to include a representative range of extant arthropods alongside a different selection of Cambrian taxa, coded for a greater number of characters. Whereas the earlier work used *Marrella* as an outgroup, the hypothesis of Briggs *et al.* (*op. cit.*) was rooted using the lobopod *Aysheaia*. This study supported the monophyly of crustaceans and suggested a very different topology within the Arachnomorpha (Fig. 3.2B). Whereas *Sarotrocercus*, *Burgessia* and *Yohoia* were still placed close to the chelicerates, the other 'great appendage' taxa, *Alalcomenaeus* and *Leanchoilia*, were found to be basal arachnomorphs. Of the taxa placed in a basal paraphyletic assemblage in the earlier study, some remained basal (*Emeraldella*, *Sidneyia*), whereas other were now more closely related to chelicerates than trilobites (*Molaria*, *Aglaspis*, *Sanctacaris*).

In a further refinement, the work of Wills *et al.* (1995, 1998*a*) coded the previously analysed taxa for many new characters and considered a small number of additional taxa, notably from post-Cambrian Palaeozoic Lagerstätten. Whilst supporting the topology of major euarthropod clades found by Briggs *et al.*, this analysis again proposed very different relationships within the Arachnomorpha (Fig. 3.2C). *Burgessia* was found to be the sister group to all other arachnomorphs, and a clade of trilobites, *Molaria* and *Naraoia* the sister group to all remaining taxa. *Cheloniellon* and *Aglaspis* were successive sister groups to chelicerates. Notably, and unlike in previous analyses, most Burgess Shale arachnomorphs formed a large clade which was placed in opposition to the ((chelicerate, *Cheloniellon*) *Aglaspis*) group.

In contrast to these studies, Bergström (1992; Hou and Bergström 1997; Bergström and Hou 1998) rejected parsimony as a phylogenetic criterion and developed an arthropod phylogeny

(Fig. 3.2D) based on a small sample of characters. The possibility of any of the selected characters evolving convergently was excluded on purely methodological grounds. Bergström's interpretations of homology are also often unclear. For example, he used leg posture, which can rarely be adequately determined in fossils, as an important character (see Edgecombe and Ramsköld 1999, p. 281). Bergström's work has been extensively criticised (e.g. Schram 1993; Briggs 1998; Cotton 1999; Edgecombe and Ramsköld 1999) and these arguments are not repeated here.

The cladistic analysis of the chelicerate stem-group presented by Dunlop and Selden (1997) included only taxa that were found to be most closely related to chelicerates by Wills *et al.* (1995, 1998*a*). The results of this analysis were largely unresolved (the published cladogram, fig. 17.3, is only one of 9450 most parsimonious trees), but supported the view of Wills *et al.* that *Cheloniellon* is more closely related to chelicerates than is *Aglaspis*. However, Dunlop and Selden (1997, p. 232) noted that cheloniellids, aglaspidids and chelicerates may not form a monophyletic group with respect to all other arachnomorphs. Emerson and Schram (1997) analysed arthropod phylogeny on the basis of Arthropod Pattern Theory (Schram and Emerson 1991). Their results are also poorly resolved, and the topology of arachnomorph taxa highly unstable across the various treatments of their data they present (compare figs 7.3A-C of Emerson and Schram). Many of their characters are difficult to interpret outside the framework of the theory.

Edgecombe and Ramsköld (1999) recently presented a cladistic study of some arachnomorph taxa in an attempt to resolve the relationships of the Trilobita. Their work was a considerable improvement on the previous studies described above in that they attempted to include a comprehensive sample of both taxa and characters, and presented detailed discussions of the homology of these characters. Their results (Fig. 3.3) supported the monophyly of the Helmetiida (*sensu* Hou and Bergström 1997), Naraoiidae and Xandarellida (see Ramsköld *et al.* 1997) within an unresolved clade also including the Trilobita. *Sidneyia*, *Emeraldella* and *Retifacies* were found to be more basal arachnomorphs on the basis of outgroup rooting with Marellomorpha.

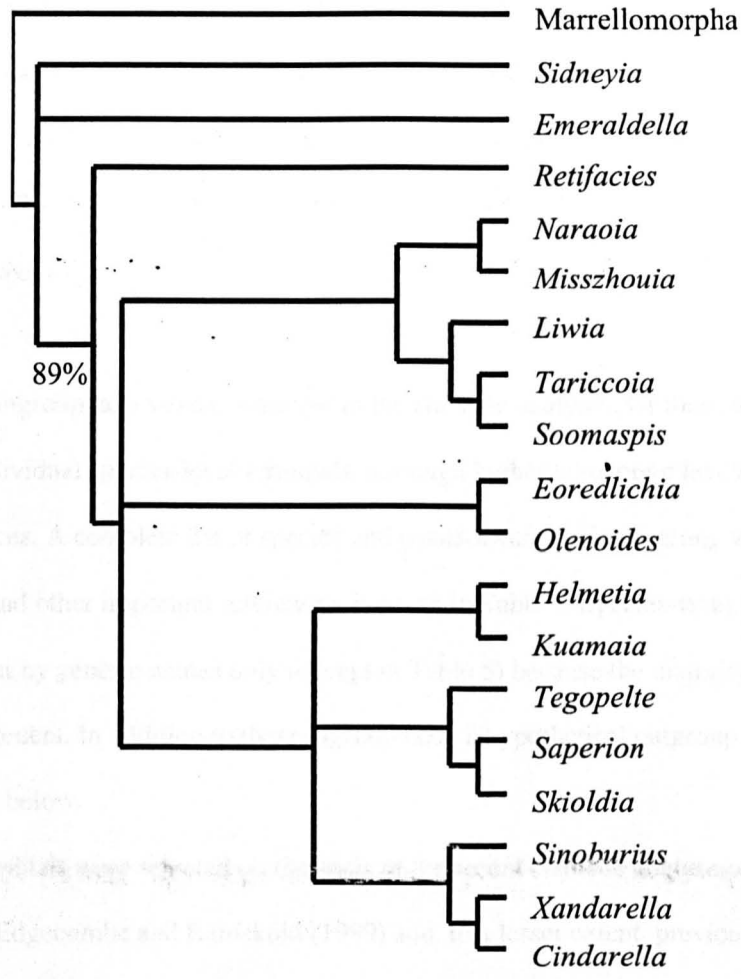


FIGURE 3.3. Majority rule consensus of 'trilobite-allied' arachnate phylogeny, after Edgecombe and Ramsköld (1999, fig. 3).

Unfortunately, Edgecombe and Ramsköld made no attempt to establish the monophyly of the group of 'trilobite-allied arachnates' they included in their cladistic analysis, and did not consider the position of the chelicerates.

CLADISTIC ANALYSIS

Taxonomic scope

Thirty-four ingroup taxa were considered in the cladistic analyses. Of these the majority were coded as individual species-level terminals, although higher taxonomic levels were employed in some instances. A complete list of species and genus-level terminals, along with details of authorship and other important references, is given in Table 5. Species-level terminals are referred to throughout by generic names only (except in Table 5) because the majority are assigned to monotypic genera. In addition to these ingroup taxa, a hypothetical outgroup was used for rooting, as discussed below.

Terminals were selected on the basis of the recent cladistic analyses of Wills *et al.* (1995, 1998*a*) and Edgecombe and Ramsköld (1999) and, to a lesser extent, previous hypotheses of arthropod relationships. The majority of taxa that have been included in an arachnomorph group by previous authors are included in this study. Notable exceptions are *Agnostus*, *Habelia*, *Molaria*, *Sanctacaris* and *Sarotrocercus*, all of which were considered by Wills *et al.* but not Edgecombe and Ramsköld, and *Offacolus* and *Phytophilaspis*, which have not been included in any previous cladistic analysis. I regard the Agnostina to be a clade within the Trilobita (e.g. Fortey 1990*a*; Fortey and Theron 1994; Wills *et al.* 1998*a*) rather than stem-group crustaceans (e.g. Shergold 1991; Bergström 1992) and their systematic position is discussed in detail in Part 4 of this thesis. The Burgess Shale taxa *Habelia* Walcott, 1912*b*, *Molaria* Walcott, 1912*b* and *Sarotrocercus*

TABLE 5. Authorship and important references for species included in cladistic analyses of arachnomorphs. Previous analyses by Briggs and Fortey (1989, 1992), Briggs *et al.* (1992, 1993), Wills *et al.* (1995, 1998) and Edgecombe and Ramsköld (1999) informed the coding of many taxa, and are not listed.

Name and authorship	Other references
Alalcomenaeus cambricus Simonetta, 1979	Briggs and Collins, 1999.
Buenaspis forteyi Budd 1999*a*	
Burgessia bella Walcott, 1912*b*	Hughes, 1975.
Cheloniellon calmani Broili, 1932	Stürmer and Bergström, 1978.
Cindarella eucalla Chen *et al.*, 1996	Ramsköld *et al.*, 1997.
Emeraldella brocki Walcott, 1912*b*	Bruton and Whittington, 1983; Briggs and Robison, 1984.
Eoredlichia intermedia (Lu, 1940)	Shu *et al.*, 1995; Ramsköld and Edgecombe, 1996.
Fortiforceps foliosa Hou and Bergström, 1997	
Helmetia expansa Walcott, 1918	Briggs *in* Conway Morris *et al.*, 1982; Briggs *et al.*, 1994.
Jianfengia multisegmentalis Hou, 1987*b*	Bergström and Hou, 1991; Chen and Zhou, 1997.
Kuamaia lata Hou, 1987*a*	Hou and Bergström, 1997; Begström and Hou, 1998; Edgecombe and Ramsköld, 1999.
Leanchoilia superlata Walcott, 1912*b*	Bruton and Whittington, 1983; Briggs and Robison, 1984.
Lemoneites Flower, 1968	Dunlop and Selden, 1997.
Liwia plana (Lendzion, 1975)	Dzik and Lendzion, 1988; Fortey and Theron, 1994; Chen *et al.*, 1997
Marrella splendens Walcott, 1912*b*	Whittington, 1971.
Mimetaster hexagonalis (Gürich, 1931)	Stürmer and Bergström, 1976.
Misszhouia longicaudata (Zhang and Hou, 1985)	Bergström and Hou, 1991; Chen *et al.*, 1997; Hou and Bergström, 1997.
Naraoia Walcott, 1912*b*	Whittington, 1977; Robison, 1984; Zhang and Hou, 1985; Chen *et al.*, 1997.
Olenoides serratus (Rominger, 1887)	Whittington, 1975*b*, 1980*b*.
Paleomerus hamiltoni Størmer, 1956	Bergström, 1971; Dunlop and Selden, 1997.
Retifacies abnormalis Hou *et al.*, 1989	Hou and Bergström, 1997.
Saperion glumaceum Hou *et al.*, 1991	Ramsköld *et al.*, 1996; Hou and Bergström, 1997.
Sidneyia inexpectans Walcott, 1911	Bruton, 1981.
Sinoburius lunaris Hou *et al.*, 1991	Hou and Bergström, 1997
Skioldia aldna Hou and Bergström, 1997	
Soomaspis splendida Fortey and Theron, 1994	Chen *et al.*, 1997.
Taricoia arrusensis Hammann *et al.*, 1990	Fortey and Theron, 1994; Chen *et al.*, 1997.
Tegopelte gigas Simonetta and Delle Cave, 1975	Whittington, 1985; Ramsköld *et al.*, 1996.
Weinbergina opitzi Richter and Richter, 1929	Stürmer and Bergström, 1981; Andersen and Selden, 1997; Dunlop and Selden, 1997.
Xandarella spectaculum Hou *et al.*, 1991	Bergström and Hou, 1991; Ramsköld *et al.*, 1997; Hou and Begström, 1997.
Yohoia tenuis Walcott, 1912*b*	Whittington, 1974.

Whittington, 1981 and the Hunsrück Slate *Magnoculus* Briggs and Bartels, 2001 are rather poorly known and hypotheses of their relationships constrained by very few characters. *Sanctacaris* Briggs and Collins, 1988 and *Offacolus* Orr *et al.*, 2000 were both originally described as having chelicerate affinities, on the basis of their supposed possession of a long head tagma, and are therefore directly relevant to this study. However, homologies among these taxa and other arachnomorphs are very difficult to establish and they are not considered in the cladistic analysis. In particular, the number and form of their head appendages is largely conjectural (e.g. Budd and Dewel, 1997). *Phyophilaspis* Ivantsov, 1999 shows a combination of features that may be homologous to those found in naraoiids (form of the pygidium), xandarellids (eye slits, overlap of anterior thoracic segments by the head shield) and Trilobita (hypostome with anterior and posterior lateral wings). It therefore potentially has a pivotal position in the phylogeny of the trilobite-allied Arachnomorpha. However, the description and interpretation of these features by Ivantsov (1999) are rather dubious, and adequately determining homology of these structures would require restudy of the material.

The Xandarellida, known only from the Chengjiang fauna, were originally described as an arachnate clade (Ramsköld *et al.* 1997). All three valid genera, *Xandarella*, *Sinoburius* and *Cindarella*, were included in the cladistic analysis of Edgecombe and Ramsköld (1999). They differ in important respects and therefore all three genera have been included, in order to test the monophyly of the group in the context of this wider analysis.

The Trilobita (excepting Agnostida) were represented in the study of Wills *et al.* (1995, 1998*a*) by *Olenoides*, the appendages of which are known from the Burgess Shale, and the Ordovician *Triarthrus* (see Cisne 1975, 1981; Whittington and Almond 1987). However, I follow Edgecombe and Ramsköld (1999) in choosing *Olenoides* and *Eoredlichia*, to represent the Trilobita. These are more basal trilobites (see e.g. Fortey 1990*a*, *b*) than *Triarthrus* and are consequently more likely to reflect the plesiomorphic trilobite state. The putative trilobite *Kleptothule* Budd, 1995 from the Early Cambrian Sirius Passet fauna of North Greenland is not

included. Its appendage morphology is unknown and homologies between exoskeletal features of this taxon and other arachnomorphs are uncertain.

The Naraoiidae or Nektaspida (reviewed above) are widely considered to be closely related to the trilobites, either as a paraphyletic assemblage of 'soft-bodied' trilobites (e.g. Shu *et al.* 1995, fig. 20B) or as the sister-group of calcified trilobites (Whittington 1977; Fortey 1997). They have been included in the Trilobita by some authors. However, Edgecombe and Ramsköld (1999) found no particularly close relationship between naraoiids and trilobites (see above). In order to test the monophyly of the group all described naraoiid genera except *Maritimella* and *Orientella* (both Repina and Okuneva 1969), which may be pseudofossils (Robison 1984*b* p. 2), are included.

Tegopelte from the Burgess Shale has also been considered a soft-bodied trilobite (Whittington 1985). Ramsköld *et al.* (1996) revised the exoskeletal morphology of *Tegopelte* and pointed out similarities to the Chengjiang taxa *Saperion* and *Skioldia.* This relationship has been confirmed by cladistic analysis (Edgecombe and Ramsköld 1999). A possible tegopeltid is also known, but undescribed, from the Soom Shale (e.g. Braddy and Almond, 1999, p. 171). The Helmetiidae, based on *Helmetia* Walcott, 1918 from the Burgess Shale, were united with the tegopeltid group in the Helmetiida by Hou and Bergström (1997), again a relationship supported by Edgecombe and Ramsköld. *Helmetia* is rather poorly known, and awaits redescription, but is very similar to *Kuamaia lata* Hou, 1987*a*, *Kuamaia muricata* Hou and Bergström, 1997 and *Rhombicalvaria acantha* Hou, 1987*a* from Chengjiang. There are no significant differences between these Chinese taxa, and their taxonomy may be over split (Delle Cave and Simonetta 1991, p. 201; Hou and Bergström 1997, p. 61, 68). The morphology of *Kuamaia lata* is known in some detail and it is coded here, along with *Helmetia* and all three tegopeltid genera.

Several other taxa were compared to *Tegopelte* and *Helmetia* by Delle Cave and Simonetta (1991, tab. 1). Of these, only *Retifacies* is known in enough detail to make coding worthwhile. *Tontoia* and *Nathorstia* (both Walcott, 1912*b*) are *nomina dubia* (see Whittington 1985, 1980*b*

respectively) and only the exoskeleton is known of *Urokodia* Hou *et al.*, 1989 and *Mollisonia* Walcott, 1912*b*. *Retifacies* has been placed near a trilobite-naraoiid-helmetiid clade (Delle Cave and Simonetta 1991; Edgecombe and Ramsköld 1999) or as sister-group to the naraoiids (Hou and Bergström 1997).

There is a long history of comparing *Emeraldella* and *Sidneyia* with chelicerates (following Størmer 1944), but the position of these taxa in cladistic studies has been highly variable (see Fig. 3.2). According to the hypothesis of Bergström, these taxa, along with the Aglaspidida and Cheloniellida, form a clade which is the sister group to the chelicerates. More usually aglaspidids or cheloniellids have been considered sister taxon to the chelicerates, and these Burgess Shale taxa more distantly related.

A cheloniellid-chelicerate clade was supported by Wills *et al.* (1995, 1998*a*) and Stürmer and Bergström (1978; also Bergström 1979) and Simonetta and Delle Cave (1981, p. 430; Delle Cave and Simonetta 1991, p. 212) placed the cheloniellid *Triopus* as ancestral to all chelicerates. Here, the Cheloniellida (*sensu* Dunlop and Selden, 1997) are represented by *Cheloniellon* , since the appendages of other cheloniellid taxa are unknown.

It has also repeatedly been suggested that chelicerates evolved from aglaspidids (e.g. Starobogatov 1990), and aglaspidids have been included in the Chelicerata by some authors (Størmer 1944; Weygoldt and Paulus 1979). The coding of aglaspidids is considered in detail in a separate section, below. *Lemoneites* (Flower, 1968) and *Paleomerus* (Størmer, 1956, also see Bergström 1971) have been assigned to the Aglaspidida by some authors (see Hou and Bergström 1997, p. 96-97). They are included to facilitate comparison with the results of Dunlop and Selden (1997). The aglaspidid-like arthropod *Kodymirus vagans* Chlupáč and Havlíček, 1965 from the Lower Cambrian of the Czech Republic (redescribed and compared to eurypterids by Chlupáč 1995) is excluded from this study because features of its morphology that are well known agree with those of *Aglaspis*. The described appendages are not reliably associated with the exoskeleton and the resulting reconstruction (Chlupáč 1995, fig. 4) is consequently highly speculative.

The phylogeny of crown-group chelicerates is a matter of considerable debate, but most authors have considered pycnogonids, xiphosurans and eurypterids to be primitive (Dunlop 1999). These hypotheses are represented by coding a generalised pycnogonid and eurypterid and the Devonian synxiphosuran *Weinbergina* (Stürmer and Bergström, 1981). *Weinbergina* is the best known synxiphosuran and is more likely to represent the primitive condition of xiphosurans than modern examples. The phylogeny of the Xiphosura has recently been studied by Anderson and Selden (1997). Coding for Eurypterida follows the recent work of Dunlop and co-workers (Dunlop and Selden 1997; Dunlop 1998; Braddy *et al.* 1999; Dunlop and Webster 1999). Coding for pycnogonids follows general works on the group (e.g. King 1973; Fry 1978), the reconstruction of the pycnogonid stem-group by Bergström *et al.* (1980) and recent work on pycnogonid phylogeny (Munilla, 1999). The pycnogonid family Ammotheidae is generally accepted as the most plesiomorphic extant group.

Two groups of Palaeozoic fossil taxa have been included in the Arachnomorpha by some authors, but considered less closely related by others. *Marrella* from the Burgess Shale and two Devonian taxa, *Mimetaster* and *Vachonisia*, have generally been considered to form a clade, the Marrellomorpha (Whittington 1971; Stürmer and Bergström 1976; Bergström 1979; Wills *et al.* 1995). This has been thought to be the sister-group to other arachnates (Stürmer and Bergström 1976), a basal schizoramian or a basal euarthropod group (see Fig. 3.2). Bergström (1979) included the Carboniferous Cycloidea in the Marrellomorpha, but there is considerable evidence that these are rather derived crustaceans (see Schram *et al.* 1997) and they are not considered further. The Burgess Shale taxon *Burgessia* has also been placed in the Marrellomorpha (Hou and Bergström 1997), but has not been found to belong to this clade in most analyses. Størmer (1944) placed *Burgessia* in a comparable systematic position to *Marrella*; he included both in the Arachnomorpha but excluded them from the Mersotomoidea. *Marrella*, *Mimetaster* and *Burgessia* were included in this study to assess whether the marellomorphs should be included in the Arachnomorpha, and the affinities of *Burgessia*.

The Cambrian 'great appendage' arthropods (the Megacheira of Hou and Bergström 1997) have been nested within the Arachnomorpha in most cladistic studies (e.g. Briggs and Fortey 1989, Wills *et al.* 1995, 1998*a*; Emerson and Schram 1997). Briggs and Fortey (1989, 1992) recognised megacheiran taxa as particularly closely related to chelicerates (Fig. 1A). Other authors (Bergström 1992; Hou and Bergström 1997) have considered megacheirans to be primitive euarthropods, or ancestral to some (but not all) crustaceans (Delle Cave and Simonetta 1991, and refs. therein). Since the monophyly of the megacheirans has not usually been supported, I have included nearly all described taxa. These include *Leanchoilia*, *Alalcomenaeus* and *Yohoia* from the Burgess Shale and *Fortiforceps* and *Jianfengia* from the Chengjiang fauna. Excluded from this study are *Actaeus* Simonetta, 1970 from the Burgess Shale, which may be a synonym of *Alalcomenaeus* (Briggs and Collins 1999), *Alalcomenaeus*? *illecebrosus* (Hou, 1987*b*, see Hou and Bergström 1997) from the Chengjiang Fauna, which is probably a chimaera (Briggs and Collins *op. cit.*), and the poorly preserved *Leanchoilia*? *hanceyi* from the Middle Cambrian of Utah (Briggs and Robison 1984).

According to the definition given above, any assessment of the limits of the Arachnomorpha needs to consider the phylogenetic position of these taxa relative to crustaceans. To this end, a generalised crustacean, which is intended to represent the plesiomorphic crustacean condition, was included as an ingroup taxon. Unfortunately, there has been considerable disagreement over the most basal crustacean group (see Wills 1997, p. 194-195; Schram and Hof 1998, p. 245-248). The coding used here largely follows Walossek and Müller's (1990, 1997, 1998; Walossek 1993) concept of the crustacean stem-group (see Fig. 3), but is intended to be conservative so that coding on the basis of other theories of crustacean origins would be similar.

Aglaspidida. The morphology of the appendages of aglaspidids is rather poorly known, having been described from three species of body fossil, *Aglaspis spinifer* Raasch, 1939, *Flobertia kochi* Hesselbo, 1992 and *Khankaspis bazhanovi* Repina and Okuneva, 1969, and trace fossil evidence

(Hesselbo 1988). Of these, the appendages of *Aglaspis*, described by Raasch (1939), Briggs *et al.* (1979) and Hesselbo (1992), are by far the best known. The appendages of *Flobertia* (described by Raasch, *op. cit.*, as *Aglaspis barrandei*, and Hesselbo *op. cit.*) agree with those of *Aglaspis*. However, those of *Khankaspis* show a quite different appendages morphology, but have only been poorly illustrated and described (Repina and Okuneva 1969). This material suggests the presence of lobate exopods with lamellate setae. This taxon is probably correctly assigned to the Aglaspididae (*cf.* Whittington 1979, p. 258; Hou and Bergström 1997) on the basis the central position of the dorsal eyes and presence of genal spines.

It remains unclear whether lamellate exopods are absent in some aglaspidids (*Aglaspis*) and present in others (*Khankaspis*), or whether the apparent differences in appendage morphology between these taxa may be due to preservational biases. A possible preservational analogue is provided by some taxa from the Chengjiang fauna, in which the exopods are very poorly preserved and the endopods of cephalic appendages preserved as impressions in the dorsal head shield in an apparently similar manner to those of *Aglaspis*. This is presumably because the endopods were more convex and more heavily sclerotised than the exopods. This mode of appendage preservation is most clearly seen in *Misszhouia longicaudata* (see Chen *et al.* 1997, figs 2a-d), but is also found in *Jianhanurius* (see Hou and Bergström 1997) and possible protaspides of *Naraoia* (Hou *et al.* 1991)

Here, a generalised aglaspidid is coded in two different ways to accommodate this uncertainty. In both codings, they are considered to have possessed a pair of antenniform appendages, following by 11 pairs of podiform endopods, on the head and first eight thoracic tergites (Briggs *et al.* 1979; Hesselbo 1988, 1992). According to one interpretation (coded as Aglaspidida 1), all the appendages are uniramous; the exopod is lost throughout. According to the other (Aglaspidida 2), exopods consisting of a single lobe fringed with lamellate setae (Repina and Okuneva 1969, p. 101-102, pl. 15, figs 1, 3-4) are present on at least some appendages, but their distribution and attachment are considered unknown.

Outgroup rooting

A hypothetical plesiomorphic euarthropod was included to allow outgroup rooting. Many of the characters considered could unambiguously be coded on the basis of recent discussions of the arthropod stem-group (Budd 1996*b*, 1997, 1999*b*). The ancestral euarthropod is here considered to have possessed a head with antennae only, and a series of post-cephalic biramous limbs with gnathobases. This implies homology of the anomalocaridid grasping appendages with antennae, and of the anomalocaridid lateral flaps with exopods. The hypothesised pattern of the evolution of plesiomorphic euarthropod characters is shown in Figure 3.4. The use of a hyothetical outgroup is somewhat unsatisfactory, but only affects the relationship between major clades (Arachnomorpha, Crustacea and Marrellomorpha), and thus the scope of the Arachnomorpha. The topology within the arachnomorphs was unaffected by the use of this outgoup, since identical results were obtained with unrooted analyses, or by rooting with Crustacea, *Marrella* or both.

Characters and coding

'Recognizing homologies is comparable to discovering new species' (Patterson 1982)

Whilst considerable effort has recently been applied to the discovery and description (or redescription) of arachnomorph taxa, with the notable exception of the work of Edgecombe and Ramsköld (1999) little attention has been given to the comparative morphology of these animals. Consequently, previous cladistic analyses (e.g. Wills *et al.* 1998*a*) have included only brief discussions of the primary hypotheses of homology (see Patterson 1982; de Pinna 1991) involved

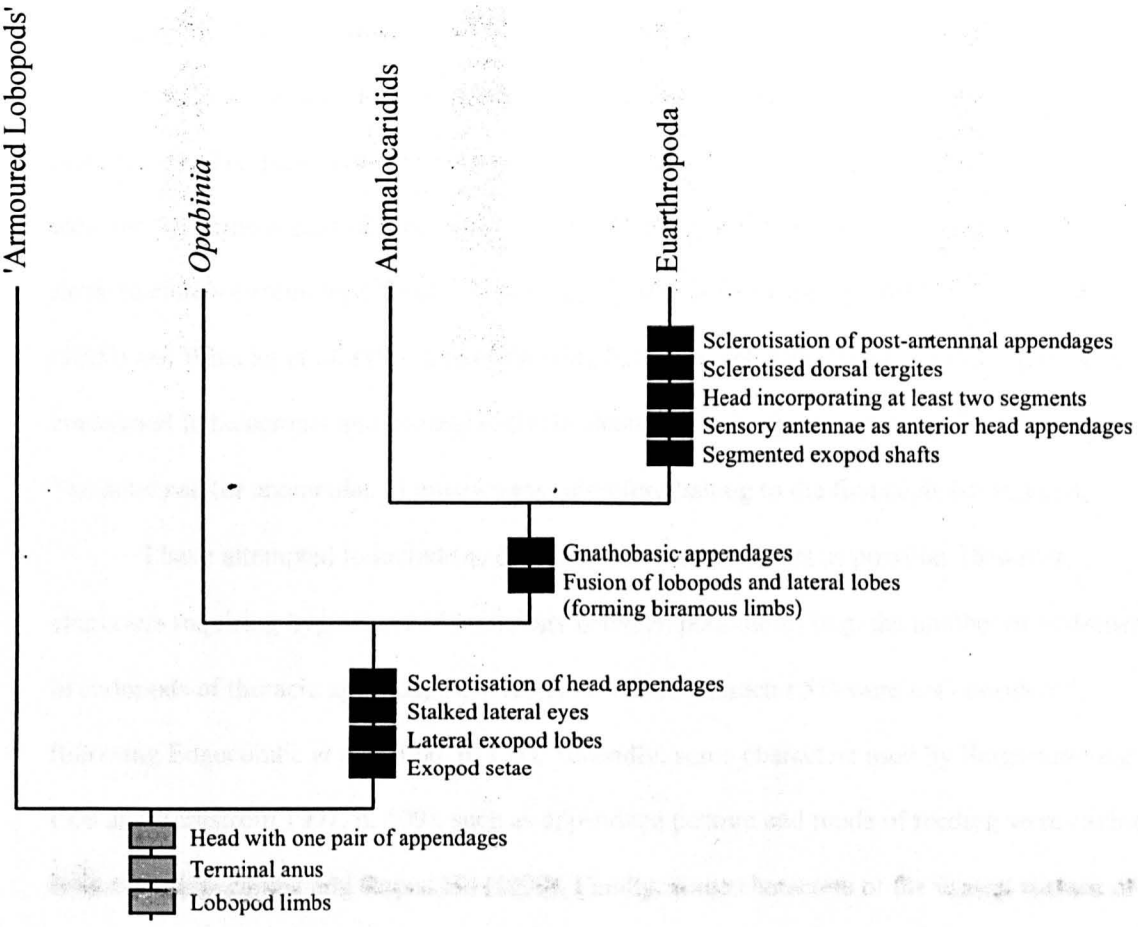


FIGURE 3.4. Reconstruction of the euarthropod stem-group used to inform coding of hypothetical outgroup. Gross topology largely follows Budd (1996*b*, fig. 9; 1997, fig. 11.10). Solid boxes indicate unambiguous apomorphies and shaded boxes character states that are plesiomorphic for the Arthropoda.

in character construction and coding. Our coding differs in many respects from those used before and a full discussion of most characters is provided. Descriptions of characters and character states, below, are arranged by organ system or body region in approximate anterior to posterior order. The distribution of character states across all taxa is shown in the data matrix in Table 6.

The previous lack of concern for homology has resulted in the terminology of morphological features in arachnomorphs being confused. Terminology developed for chelicerates, trilobites and crustaceans has variously been applied to taxa included in this study. Some attempt is made to clarify terminology herein. Where appropriate our terminology follows Edgecombe *et al.* (2000) and Wheeler *et al.* (1993), but following Scholtz (1997) the protocerebral 'segment' is considered to be acronal and consequently the deutocerebral segment to be the first true segment. The antennae (or antennulae of crustaceans) therefore belong to the first cephalic segment.

I have attempted to include as complete a set of characters as possible. However, characters requiring hypotheses of homology between podomeres (e.g. the number of podomeres in endopods of thoracic appendages, Wills *et al.* 1998*a* character 51) were not considered, following Edgecombe *et al.* (2000, p. 157). Secondly, some characters used by Bergström (e.g. Hou and Bergström 1997, p. 109), such as appendage posture and mode of feeding were excluded, following Edgecombe and Ramsköld (1999). Finally, some characters of the ventral surface of the head were not coded, as discussed below and illustrated in Figure 3.7. No attempt has been made to include all potential synapomorphies for the Chelicerata, the status of many of which is hotly debated (see e.g. Shultz 1990; Dunlop and Selden 1997; Weygoldt 1998; Wheeler and Hayashi 1998; Dunlop 1999; Edgecombe *et al.* 2000).

Two methods for the coding of inapplicable characters in phylogenetic analysis have been used. Firstly, inapplicable character states can be coded as missing data. A complex structure may comprise characters: 'absent/present' and 'state1/state2', with taxa lacking the structure coded as absent for the first character and as missing data for the second. Some authors have regarded this method as problematic because it may lead to reconstruction of impossible ancestral states, and

TABLE 6. Data matrix for cladistic analyses of arachnomorphs. '?' and '-' indicate missing data and inapplicable characters, respectively. Letters indicate multistate uncertainty codings, as follows: A = (34), B = (02), C = (01), D = (134), E = (12).

	1	2	3	4	5	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234
OUTGROUP	0000000000	0?0--00000	00000040-0	0000000000	000-0000--	-0-0
Aglaspidida 1	001A000001	0-----0001	00000000-1	1001000000	0012110?--	-101
Aglaspidida 2	00?A00000?	010--?0101	00000000-1	1001000000	0012110?--	-101
Alalcomenaeus	1113-20100	010--10000	000000D0-0	1001000000	000-0101--	-110
Buenaspis	??????????	0???????1?B	??0010?0-0	10?1000010	000-0?1110	10-0
Burgessia	0003000000	010--00012	-0000040-0	000?002000	000-0001--	-100
Cheloniellon	0014000001	010--00101	00000010-0	1001000001	0010110?--	-0-1
Cindarella	0006000000	0110000110	00000010-0	1011002100	010-101100	00-0
Crustacea	0003000000	000--01000	00000040-0	0000000000	000-0?00--	-100
Emeraldella	0015000000	0110000102	-0000000-0	1001000000	00111101--	-101
Eoredlichia	0003000010	0110000100	1000003111	1002000000	000-101100	10-0
Eurypterida	1116-11001	110--10101	0001004100	1001000000	00130101--	-100
Fortiforceps	0114-00000	010--10010	000000D0-0	1001000000	000-0101--	-110
Helmetia	???3????10	?1????01?0	0?000120-0	1002000001	100-001101	00-0
Jianfengia	1114-10000	010--10110	000000D0-0	1001000000	000-0101--	-100
Kuamaia	000?0000?0	0110100100	01000120-0	1002000001	100-001101	00-0
Leanchoilia	1113-20100	010--1011B	000000D0-0	1001000000	000-1101--	-100
Lemoneites	??????????	0?????????1	?00??00??1	10?1000000	00120?0?--	-10?
Liwia	0???1?????	0?????????	0????0???0	10?1001010	000-0?1110	00-0
Marrella	0011000000	000--01002	-000?000-0	000?002000	000-0000--	-0-0
Mimetaster	0012000000	000--0101C	000??000-0	0001002000	000-0000--	-0-0
Misszhouia	0003000010	0111000100	00000010-0	11--200010	000--01100	10-0
Naraoia	0003100010	0111000100	00000010-0	11--200010	000--01100	?0-0
Oleroides	0003000010	0110000101	1000003111	1002000000	000-011100	00-0
Paleomerus	??????????	0????????1	0000?0???1	10??000000	000-0?0?--	-10?
Pycnogonida	1114-11001	11----0011	00010040-0	000?000000	001?0000--	-100
Retifacies	0003000000	010--00100	00000000-0	1001000000	000-101100	0100
Saperion	0???2?????	0?10100110	01000120-0	11--11--00	100--?1100	10-0
Sidneyia	0010100001	010--00100	0000000??0	1001000000	00121101--	-101
Sinoburius	0004000000	01????01?0	01100010-0	1001002100	010-001101	00-0
Skioldia	0???2?????	0????????0	01000120-0	11--11--00	100--?1100	10-0
Soomaspis	??????????	01???????B	000010?0-0	10?1001010	000-0?1110	10-0
Tariccoia	??????????	01???????B	000010?0-0	10?1001010	000-0?1110	10-0
Tegopelte	000?0000??	01????011?	0?0001E0-0	10--E1--00	?00--01100	10-0
Weinbergina	1116-11001	110--10101	0001004100	1001000000	00120101--	-100
Xandarella	0004000000	0111000100	00100010-0	1011002100	010-10110?	00-0
Yohoia	1114-10001	110--10?10	000000D0-0	1001000000	00120101--	-110

hence unjustified trees (Platnick *et al.* 1991). The alternative is to code the second character as a third 'not applicable' state in taxa that lack the structure. These methods are equivalent to Pleijel's (1995) coding methods C and B, respectively. In this study, inapplicable characters are treated as missing data for most analyses, because coding them as a distinct character state reduces character independence and effectively weights the inapplicable character and hence could result in them dominating the analysis. The effects of this assumption were investigated by using a distinct character state in some analyses (see Results below) and inapplicable character are shown as distinct to 'true' missing data (using the symbol '-') in the matrix (Table 6). Unless otherwise stated, a coding of '-' was treated as missing data and identical to a coding of '?'.

Anterior cephalic appendages and head segmentation

1. Appendages of the first segment (antennae): 0- present; 1- absent.

The majority of taxa considered in this study possess a single pair of long uniramous multiarticulated antennae at the anterior of the head, which presumably had a sensory function, as found in Crustacea, Myriapoda and Insecta. These appendages are likely to be a synapomorphy of the Euarthropoda (e.g. Scholtz 1997; Walossek and Müller 1997) and the outgroup is therefore coded as State 0. The anteriormost head appendages of most Cambrian megacheiran arthropods, which have been called 'great appendages' following Walcott (1912*b*), consist of a small number of robust, spinose podomeres. Uniquely, *Fortiforceps* has a pair of short antennae anterior to the 'great appendages' (Hou and Bergström 1997, 34-38). It appears likely, therefore, that the 'great appendages' are the appendages of the second cephalic segment, and the antennae are lost in megacheirans other than *Fortiforceps.* This, of course, depends on recognising the 'great appendages' as homologous in all of these taxa, as discussed below (Character 2). Homology of

the megacheiran anterior appendages with the second cephalic appendages of trilobites was previously suggested by Størmer (1944, p. 124), on the basis of their post-oral position.

The classical view of chelicerate head segmentation maintains that they too have lost the antennae and the chelicerae are the appendages of the second cephalic segment. The most recent revision of arthropod phylogeny has supported this homology (Edgecombe *et al.* 2000, p. 157, character 44), which is based largely on neuroanatomy. The 'cheliceroneuromer' which ennervates the chelicerae seems to be homologous with the tritocerebrum, associated with the second cephalic appendage pair of mandibulates (see Weygoldt 1979; Winter 1980). This view is also supported by the presence of pre-cheliceral appendages in a pycnogonid larva (Larva D of Müller and Walossek 1986) from the Upper Cambrian of Sweden (Walossek and Müller 1997; Dunlop 1999). Thus, despite recent claims that chelicerae are homologous to the antennae of mandibulates, based on patterns of Hox gene expression (Damen *et al.* 1998; Telford and Thomas 1998), morphological evidence strongly supports the view that chelicerates have lost the antennae. The Hox gene evidence suffers from a lack of comparative data from diverse mandibulates, especially primitive crustaceans (see Akam 2000; Wheeler *et al.* 2000), and the use of Hox gene expression boundaries as markers for segmental homology has been criticised (Abzhanov *et al.* 1999). Wills *et al.* (1998*a*, p. 43, 48) considered the chelicerae to be appendages of the second, deutocerebral, segment and, curiously, in support of this cited Schram (1978) who unambiguously followed the homology scheme used here.

The anteriormost appendages of *Aglaspis* were originally described as chelicerae (Raasch 1939), which lead to their classification in the Chelicerata (e.g. Størmer 1944). However, the morphology of these appendages (see Briggs *et al.* 1979) is more similar to that of antennae. They are narrow relative to the thoracic endopods, of relatively even diameter proximally and the podomeres are apparently weakly defined. Hesselbo (1988, 1992) has also argued that the anterior appendages of *Aglaspis* are likely to be antennae. The distal parts are unknown (and hence so is their length, *cf.* Wills *et al.* 1998*a*, p. 58) and there is no evidence that they were chelate, contrary

to the coding of Wills *et al.* (1998*a*, character 31). Nothing is known about the anterior appendages of *Buenaspis*, *Lemoneites* or *Paleomerus*, and this character is accordingly coded as missing data in these taxa.

2. Form of endopod of appendages of the second segment: 0- pediform; 1- anteriorly directed raptorial appendage with reduced number of podomeres and terminal podomeres bearing spines on distal margins.

As discussed above, chelicerae and 'great appendages' are both likely to represent the appendages of the second segment. They also differ from the primitive biramous euarthropod limb in similar ways and are therefore likely to be homologous as modifications of these appendages. The homology of 'great appendages' and chelicerae was originally proposed by Henriksen (1928) and supported by Størmer (1944) but, to our knowledge, no modern author has discussed this possibility.

Both 'great appendages' (Figs 3.5A, D-E) and chelicerae (Figs 3.5B-C) are equipped with strong spinose projections on the outer (dorsal) side of the distal margins of terminal podomeres that are lacking on proximal podomeres. Secondly, the number of podomeres in both chelicerae and 'great appendages' is more-or-less reduced compared to the number in the endopods of biramous limbs. In the case of 'great appendages' they are significantly more robust than those of posterior endopods, a situation that is matched in some chelicerates. The homology of the 'great appendages' of *Alalcomenaeus*, *Leanchoilia*, *Yohoia*, *Jiangfengia* and *Fortiforceps* is supported by all of these features, and is widely accepted (e.g. Wills *et al.* 1998*a*, character 31; Hou and Bergström 1997; Bergström and Hou 1998; Hou 1987*a*). Only Hou and Bergström (1991, p. 183) have suggested, albeit in passing, that the 'great appendages' of all these taxa may be convergent, a view they appear to have reversed.

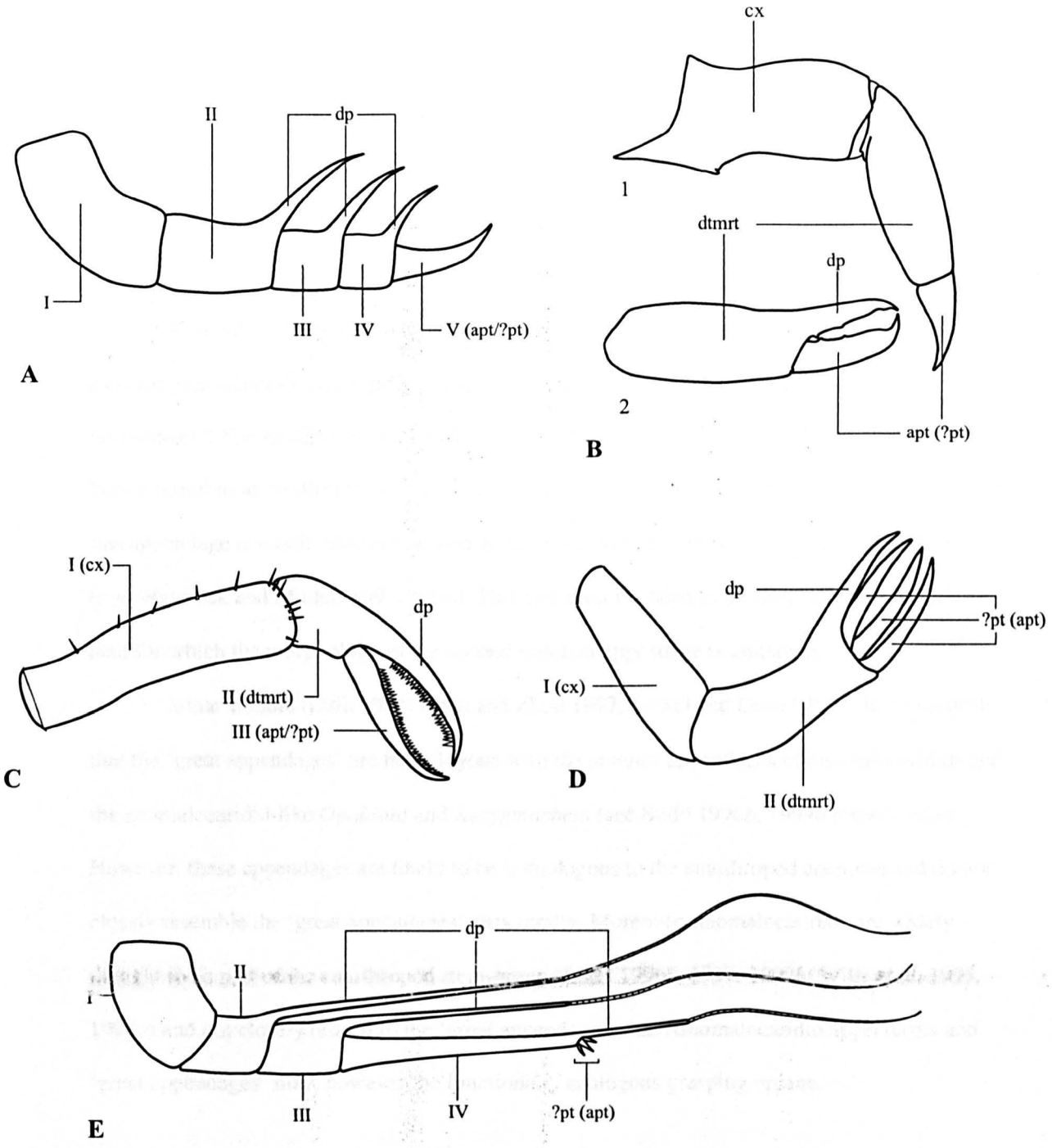


FIGURE 3.5. Diagrammatic reconstructions of raptorial second segment appendages in lateral view (except where otherwise stated) and approximate life orientation, showing suggested homology of appendage elements (in brackets). Roman numerals indicate position in the podomere series and do not necessarily imply homology. A. 'Great appendage' of *Fortiforceps,* after Hou and Bergström, 1997. B. Left chelicera of *Leiobunum aldrichi* (Arachnida: Opiliones), 1, in medial perspective and 2, distal parts in anterior perspective, after Shultz, 2000. C. Chelifore of *Nymphon* (Pycnogonida), after Child, 1997. D. 'Great appendage' of *Yohoia*, after Whittington, 1974, text-fig. 2. E. 'Great appendage' of *Leanchoilia*, modified after Bruton and Whittington, 1983. Not to scale. Abbreviations: apt, apotele (probably homologous with the mandibulate pretarsus); cx, coxa; dtmrt, deutomerite; pt, pretarsus.

The endopods of the appendages of other taxa are locomotory legs which either lack strong spines or have spinose extensions that are invariably on the medial (ventral) surface and are stronger on proximal podomeres than distal ones (e.g. *Misszhouia*, Fig. 3.6). In the latter case, these spines form part of the feeding system, along with the gnathobases, and are often located around the middle of the podomere rather than limited to the distal margin. These endopods are directed ventrolaterally, as opposed to anteriorly in the case of both chelicerae and 'great appendages'. The modified second appendages of *Marrella* resemble this plesiomorphic condition, here referred to as 'pediform', except in their anterolateral orientation. In some Recent crustaceans this appendage is modified into a second antenna, but in stem-group crustaceans it is pediform (e.g. Walossek and Müller, 1997, 1998). This character is coded as missing data in a number of taxa for which the morphology of the second segment appendage is unknown.

Some authors (Dzik 1993; Chen and Zhou 1997; Dewel and Dewel 1997) have suggested that the 'great appendages' are homologous with the anterior appendages of anomalocaridids and the anomalocaridid-like *Opabinia* and *Kerygmachela* (see Budd 1996*b*, 1999*b* respectively). However, these appendages are likely to be homologous to the euarthropod antennae and do not closely resemble the 'great appendages' structurally. Moreover, anomalocaridids are widely thought to be part of the euarthropod stem-group (Budd 1996*b*, 1997, 1999*b*; Wills *et al.* 1995, 1998*a*) and not closely related to the 'great appendage' taxa. Amomalocaridid appendages and 'great appendages' may, however, be functionally analogous grasping organs.

3. Exopod of appendages of the second segment: 0- present; 1- absent or much reduced.

The raptorial appendages of the second segment (chelicerae and 'great appendages') are uniramous, as are the corresponding pediform appendages of *Marrella*, *Mimetaster*, *Emeraldella*, *Cheloniellon* and *Sidneyia*. The plesiomorphic euarthropod state is found in most other arachnomorphs, including trilobites, where the biramous second segment appendages are

undifferentiated from those of posterior segments (Edgecombe *et al.* 2000, character 78). The exopods of these appendages are also present in basal members of the crustacean crown-group (Edgecombe *et al.* 2000, character 79) and in stem-group crustaceans (Walossek 1993; Walossek and Müller 1997, 1998).

4. Number of segments incorporated into the head: 0- 1; 1- 2; 2- 3; 3- 4; 4- 5; 5- 6; 6- 7.

The coding of this character by Edgecombe and Ramsköld (1999, character 2) explicitly referred to the number of limb pairs present in addition to the antenna. Here, the number of post-acronal segments present in the head is coded following Wills *et al.* (1998*a*, character 29). In taxa that lack an antenna the number of somites is inferred to be one greater than the number of cephalic appendage pairs (*cf.* Wills *et al.* 1998*a*), as described above.

Stürmer and Bergström (1978) suggested that the head of *Cheloniellon* is defined primarily on the basis of appendage tagmosis, rather than the fusion of segments under a single head-shield (cf. Hou and Bergström 1997, p. 98-99). According to this view, the head consists of both the cephalic tergite and the anteriormost free tergite that share uniramous, gnathobasic appendages. Wills *et al.* (1998*a*) coded *Cheloniellon* as having 6 somites incorporated into the head and therefore presumably accepted this suggestion. There is no evidence that the first free tergite of *Cheloniellon* was incorporated into the head (except perhaps functionally), and so I prefer to code the number of somites under the cephalic shield. In *Sidneyia*, there is a series of uniramous, strongly gnathobasic appendages, similar to those of *Cheloniellon*, posterior to the head shield. All of these appendages would presumably have to be considered part of the head based on appendage differentiation, according to the view of Stürmer and Bergström (1978). Some autapomorphic states are included (0 for *Sidneyia*, 1 for *Marrella*, and 6 for *Emeraldella*) since these will become informative if the character is treated as ordered.

A novel form of cephalic tagmosis was described by Edgecombe and Ramsköld (1999, p. 265). I accept their suggestion that in trilobite-like taxa the fourth pair of biramous cephalic appendages was directly under the cephalo-thoracic junction. This may explain previous confusion about the number of such appendages incorporated into the trilobite cephalon (e.g. Cisne 1975; Whittington 1975*a*; Bergström and Brassel 1984). However, Edgecombe and Ramsköld accepted the view of Chen *et al.* (1997, p. 7) that only the first three biramous limbs of *Misszhouia* were structurally and functionally part of the head. It seems more acceptable, therefore, to code these taxa as having only four post-acronal somites than to use the coding scheme of Edgecombe and Ramsköld (1999). The partial integration of the first thoracic somite under the head shield could be considered to be a form of overlap of the trunk by the headshield (i.e. a distinct state of character 9 of Edgecombe and Ramsköld 1999, or Character 36 herein). Derived states of this character would then potentially be synapomorphic for a clade including xandarellids, naraoiids, helmetiids, tegopeltids and trilobites. However, since the degree of overlap in taxa with the fourth biramous appendages under the cephalo-thoracic articulation is identical to that found between thoracic tergites (State 0 of Character 36), it is preferred to regard this as a distinct character (Character 9, below).

The coding of *Alalcomenaeus* as having 4 post-acronal somites by Wills *et al.* (1998*a*) is accepted here, but for different reasons. Briggs and Collins (1999) have recently demonstrated that *Alalcomenaeus* possessed two pairs of biramous appendages on the head in addition to the great appendates. This would equate to three head somites according to the homology scheme of Wills *et al.* (*op. cit.*). Here, the antennae are inferred to be lost and therefore four segments incorporated into the head.

Recently, a number of authors have agreed that the plesiomorphic condition for euarthropods is a four segment head, as found in stem-group crustaceans (Scholtz 1997; Walossek 1996; Walossek and Müller 1997, 1998; Edgecombe *et al.* 2000). However, reconstruction of the euarthropod stem-group clearly indicates that even crownward taxa had a head consisting of only

the antennal segment and acron, as found in tardigrades and onychophorans. It seems, therefore that the four segment head is plesiomorphic only for crown-group euarthropods. Some fully arthropodised fossil taxa also have a shorter head that may be plesiomorphic, such as the two segment head of *Marella* and *Mimetaster*. *Retifacies* is coded following the recent redescription of Hou and Bergström (1997), rather than on the basis of the coding by Edgecombe and Ramsköld (1999), for which they provide no explanation. A partial uncertainty coding is used for *Aglaspis*, in which the number of post-antennal cephalic appendages is either three or four (Briggs *et al.* 1979)

5. Orientation of the antennae: 0- directed anterolaterally; 1- strongly deflected laterally; 2- placed well inside shield margin, curving posteriorly from a transverse proximal element.

This character was adequately described by Edgecombe and Ramsköld (1999, character 3) and their coding is followed for the taxa they considered. The anterior appendages of *Aglaspis* (see Character 1) are clearly directed anterolaterally, and it is presumed that they continued past the head shield margin. The anterior appendages of arthropod stem-group taxa such as *Aysheaia*, *Kerygmachela* and *Anomalocaris* are either directed anterolaterally or ventrally, but are not strongly deflected laterally. The outgroup is therefore coded as State 0. This character is coded as missing data for taxa where the presence of antennae is equivocal (those coded as missing data for Character 1), and as inapplicable to taxa where the antennae are considered absent (coded as State 1 for Character 1).

6. Length of distal spines on terminal podomeres of endopods of second segment appendages: 0- absent or shorter than podomeres; 1- subequal to length of podomeres; 2- longer than the entire podomere series.

The spinose projections of the raptorial appendages described above vary in length. In chelicerae (Figs 3.5B-C) and some 'great appendages' (e.g. those of *Yohoia*, see Fig. 3.5D) the most distal spine is equal in length to the spinose terminal podomere, forming a chelate structure. In other taxa (*Fortiforceps*, Fig. 3.5A) the spines are short relative to the lengths of the podomeres or (*Alalcomenaeus*, *Leanchoilia*, Fig. 3.5E) extremely long, so that the spines are much longer than the entire podomere series. As described above, in taxa with pediform endopods of the second segment appendages, spines on the distal podomeres are short or entirely absent.

7. Chelicerae: 0- absent; 1- present.

Despite their similarities to 'great appendages', the chelicerae of the euchelicerates and chelifores of the pycnogonids are clearly distinct, and have been widely recognised as a chelicerate synapomorphy. Chelicerae differ from any 'great appendages' by the combination of a generally smaller number of podomeres, the presence of only a single terminal element and only a single spinose projection on the dorsal side of the podomere series (see Fig. 3.5). Amongst extant chelicerates, only the pycnogonid *Pallenopsis* has chelicerae of four podomeres, comparable to the number in 'great appendages'. Bergström *et al.* (1980) considered that the chelifores of the Devonian pycnogonid *Palaeoisopus* also consisted of four segments, but this is not well supported by their figures (e.g. figs 16-17).

8. Distal spines of second segment endopods terminating in annulated flagellae: 0- absent; 1- present.

It has widely been recognised (e.g. Størmer 1944; Simonetta 1970; Bruton and Whittington 1993; Briggs and Collins 2000) that the terminal parts of the extended spines of *Alalcomenaeus* and *Leanchoilia* formed annulated flagellae. Nothing similar is known from homologous appendages

of any other arthropod, although similar processes may have operated in the transformation of the endopod as a whole into the second antennae of derived crustaceans and in the origin of multiramous antennulae (first antennae) in malacostracans.

Posterior appendages

9. Appendages of first thoracic somite underneath the cephalo-thoracic articulation: 0- absent; 1- present.

For discussion of this character, see Character 4 (above) and Edgecombe and Ramsköld (1999, p. 265, character 2).

10. Exopods of appendages of third to fifth segments: 0- present; 1- reduced or absent.

A number of taxa have uniramous appendages on the third to fifth segments. In most these segments are incorporated into the head (*Yohoia*, chelicerates), but in others all (*Sidneyia*) or some (*Cheloniellon*) of these segments are post-cephalic. In all cases the appendage is morphologically similar to the endopods of biramous limbs of other taxa and/or other segments, and it is interpreted that the exopod is lost.

11. Endopods of thoracic appendages: 0- present; 1- reduced or absent.

The opisthosomal appendages of chelicerates lack endopods or have the endopods much reduced (e.g. *Limulus*, Siewing 1985, fig. 838). A situation that is also found in the uniramous thoracic

appendages of *Yohoia* (Whittington 1974). It has been suggested that *Helmetia* (Briggs *et al.* 1994) lacks endopods, but pending a redescription of this genus, and considering that they have been documented in the otherwise very similar *Kuamaia*, this is coded as uncertain.

12. Exopod shaft of numerous podomeres each bearing a single seta: 0- present; 1-absent.

The exopods of crustaceans (at least plesiomorphically, see e.g. Walossek and Müller 1998, figs 5.5, 5.6) and of *Marrella* and *Mimetaster* have multi-annulated shafts, with each podomere bearing a single seta. In other taxa the exopod shafts consist of one of two lobes bearing numerous setae.

The polarity of exopod segmentation is uncertain. The lateral flaps of stem-group arthropods such as *Opabinia* (Whittington 1975*b*; Budd 1996*b*) and anomalocaridids (e.g. Hou *et al.* 1995) are certainly unsegmented but, as suggested by Budd's (*op. cit.*, fig. 8) reconstruction, this does not necessarily suggest the form of the primitive euarthropod exopod. Rather, segmentation may have been a result of the sclerotization of the cuticle of the exopod shaft. The outgroup was coded as uncertain for this character. According to the first interpretation of aglaspidid appendage morphology (coded as Aglaspidida 1), the exopods are lacking on all appendages, and consequently this and all other characters describing exopod morphology are coded as inapplicable.

13. Exopod shaft differentiated into proximal and distal lobes: 0- absent; 1- present.

Ramsköld and Edgecombe (1996; Edgecombe and Ramsköld 1999, character 26) have recently discussed the distribution of the trilobite-type bilobate exopods recognised by this character (Figure 3.6A). Among taxa included here that were not considered by Edgecombe and Ramsköld (*op. cit.*), exopods consist either of a single flattened lobe or a homonomous series of podomeres

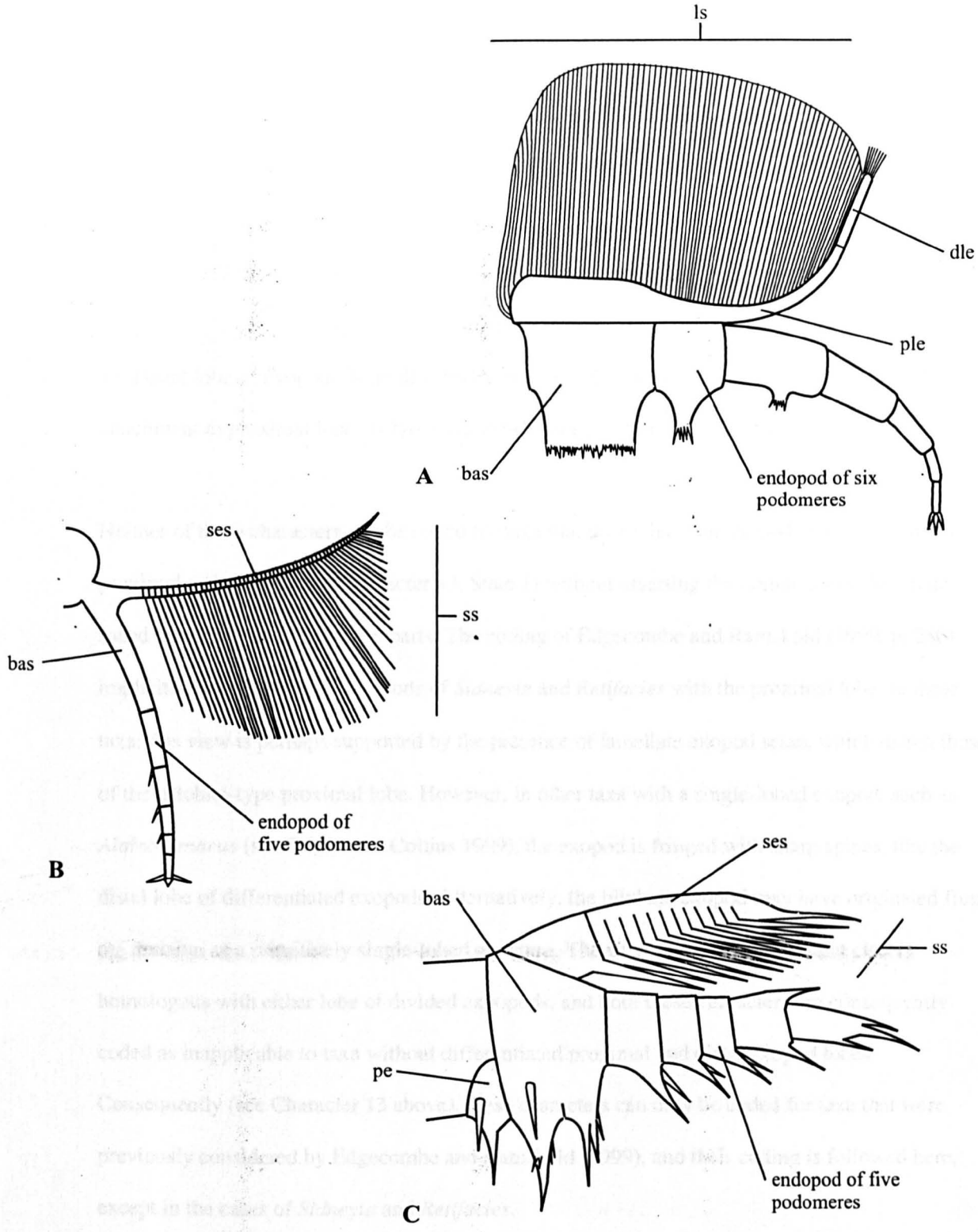


FIGURE 3.6. Diagrammatic reconstructions of arachnomorph (A) and non-arachnomorph (B-C) biramous appendages. A. The 'trilobite-type' biramous appendage of *Misszhouia longicauda*, after Chen et al. (1997). B. Appendage of *Marrella splendens*, after Whittington (1971). C. Appendage of the stem-lineage crustacean *Martinssonia elongata*, after Müller and Walossek (1997, 1998). Not to Scale. Abbreviations: bas, basis; dle, distal lobe of exopod shaft; ls, lamellar exopod setae; pe, proximal endite or pre-coxa; ple, proximal lobe of exopod shaft; ses, segmented exopod shaft; ss, spinose exopod setae.

(Figure 3.6B-C). No stem-group euarthropod has a bilobate exopod, and the outgroup is consequently also coded as State 0.

14. Proximal lobe of exopod: 0- flattened lobe; 1- slender shaft.

15. Distal lobe of exopod: 0- small to moderate sized flap, with short to moderately long attachment to proximal lobe; 1- large, teardrop shaped, with long attachment to proximal lobe.

Neither of these characters can be coded for taxa that do not have an exopod differentiated into proximal and distal lobes (Character 13, State 1) without asserting the homology of the single-lobed exopod with one of these parts. The coding of Edgecombe and Ramsköld (1999, p. 280) implicitly homologizes the exopods of *Sidneyia* and *Retifacies* with the proximal lobe. In these taxa, this view is perhaps supported by the presence of lamellate exopod setae, which match those of the trilobite-type proximal lobe. However, in other taxa with a single-lobed exopod, such as *Alalcomenaeus* (see Briggs and Collins 1999), the exopod is fringed with sharp spines, like the distal lobe of differentiated exopods. Alternatively, the bilobate exopod may have originated from the division of a primitively single-lobed structure. The single-lobed exopod is not clearly homologous with either lobe of divided expopods, and both these characters are consequently coded as inapplicable to taxa without differentiated proximal and distal exopod lobes. Consequently (see Character 13 above), these characters can only be coded for taxa that were previously considered by Edgecombe and Ramsköld (1999), and their coding is followed here, except in the cases of *Sidneyia* and *Retifacies*.

16. Exopod shaft a deep rounded flap: 0- absent; 1- present.

All bilobate (Character 13) and segmented (Character 12) exopod shafts are long (trans.) and relatively narrow (dorsoventrally) structures (see Fig. 3.6) whereas some single lobed exopod shafts have the form of rounded flaps. These flap-like exopod shafts are large compared to the length of the setae and at least half as deep as they are long. This appendage structure is found in chelicerates and 'great appendage' arthropods.

17. Medially directed exopod setae: 0- absent; 1- present.

Walossek and Müller (1998, p. 194) suggested that the tilting of exopod setae towards the endopod in post-antennular limbs with a multi-annulated exopod was an autapomorphy uniting crustaceans and all members of the crustacean stem-group (the crustacean total group *sensu* Ax 1986; see Figure 3.6C). This character is shared with the marellomorphs *Marrella* and *Mimetaster* (see Figure 3.6B; Stürmer and Berström 1976; Bergström 1979, figs 1.3A-B). In other taxa, the setae either surround the entire margin of the exopod shaft or are directed dorsally (Figure 3.6A). The identification of setae on the dorsal surface of the lateral flaps in *Opabinia* (Budd 1996*b*) suggests that the condition in marellomorphs and crustaceans is derived.

18. Lamellate exopod setae: 0- absent; 1- present.

Lamellate exopod setae, originally described from trilobites, are a classic synapomorphy of the Arachnomorpha (see e.g. Bergström 1992; Hou and Bergström 1997, p. 42-43). They are perhaps best known from *Misszhouia* (see Chen *et al.* 1996, Hou and Bergström 1997; Figure 3.6A). These setae differ from the more spinose setae of other taxa (Figure 3.6C) in that they are wide and flat and imbricate over the length of the exopod shaft. The setae of *Marrella* (Figure 3.6B) and similar taxa have variously been considered lamellate (Bergström 1979) or non-lamellate (Bergström 1992). Since they do not imbricate and do not seem to be strongly flattened (Whittington 1971;

Stürmer and Bergström 1976, fig. 9a), *Marrella* and *Mimetaster* are coded as State 0. The setae of *Helmetia*, as shown in Briggs *et al.* (1994, fig. 141), seem to be of the lamellate type. The setae of *Sinoburius* have been described by Hou and Bergström (1997, p. 85) as similar to those of *Misszhouia*. Only the setae are known of the appendages of *Buenaspis* (Budd 1999*a*), and also these appear to be of the trilobite-type.

The homology of the book-gill lamellae of xiphosurans with lamellar setae has been supported by some authors (e.g. Walossek and Müller 1997, p. 149; Edgecombe *et al.* 2000, p. 174), but rejected by others (Stürmer and Berström 1981) on the grounds that *Weinbergina* possesses *Limulus*-like gill lamellae and fringing setae. Book-gills have also been described from a eurypterid (Braddy *et al.* 1999). There are certainly major morphological differences between book-gills and trilobite-type exopods. Following most recent opinion, and pending further study, *Weinbergina* and Eurypterida are coded as possessing lamellate setae.

The form of the setae of *Yohoia* is uncertain (Whittington 1974); the spinose setae seen in the most common reconstruction (Gould 1989; Briggs *et al.* 1994) are not justified by the specimens. Amongst other great appendage arthropods the form of the setae appears to be variable. Those of *Jianfengia* (see Chen and Zhou 1997, p. 74) and *Leanchoilia* (see Bruton and Whittington 1982) being lamellate, those of *Fortiforceps* (Hou and Bergström 1997) and *Alalcomenaeus* (Briggs and Collins 1999) spinose and less densely packed.

19. Gnathobase on basis and/or prominent endites on endopod: 0- present; 1- absent.

The distribution of this character in the majority of terminals has previously been discussed by Edgecombe and Ramsköld (1999, character 29) and Wills *et al.* (1998*a*, characters 36, 59) and their coding is followed here. The presence of gnathobases on the appendages of some anomalocaridids (Hou *et al.* 1995) and their general distribution amongst non-arachnomorph euarthropods suggests that State 0 is plesiomorphic. The homology of the various endites and

gnathobasic structures found in euarthropods is in need of careful assessment, and a very general coding (following Edgecombe and Ramsköld) is therefore used for this character.

Eyes

20. Position of lateral facetted eyes: 0- ventral and stalked; 1- dorsal and sessile; 2- absent.

This character is largely coded as described by Edgecombe and Ramsköld (1999, character 4). Partial uncertainty coding is used for a number of taxa where the dorsal surface is known, but the ventral morphology is not, and the presence of ventral eyes therefore cannot be discounted. For example, there is good evidence that *Leanchoilia* lacked dorsal sessile eyes, but ventral stalked eyes may have been present (as in *L. hanceyi*, see Briggs and Robison 1984), and a (02) partial uncertainty coding is used. This is also the case in many naraoiids, such as *Buenaspis*. However, only the outline of the head shield of *Liwia* is known, and the absence of dorsal eyes in the reconstruction of Dzik and Lendzion (1988) is conjectural. It is unclear whether the autapomorphic condition of stalked dorsal eyes in *Mimetaster* (see Stürmer and Bergström 1976) is homologous with State 0 or State 1, and a partial uncertainty coding is also used.

Whittington (1974) was somewhat equivocal about the nature of the lateral lobes anterior to the head shield of *Yohoia*. These more closely resemble the ventral stalked eyes of *Alacomenaeus*, as recently described by Briggs and Collins (1999), than either Whittington's (1974) or subsequent (e.g. Gould 1989, fig. 3.18; Briggs *et al.* 1994, fig. 153) reconstructions suggest. In a well preserved specimen showing the dorsal aspect (USNM 57696, Whittington 1974, pl. 2, figs 1-3) and in a laterally compressed specimen (USNM 57694, pl. 1, fig. 1) they are clearly seen to be stalked and relatively small lobate structures. That these structures are likely to

represent stalked ventral eyes was reflected in the coding of Wills *et al.* (1998*a*, characters 26 and 27).

21. Visual surface with calcified lenses, bounded with circumocular suture: 0- absent; 1- present.

22. Dorsal bulge in exoskeleton accommodating drop-shaped ventral eyes: 0- absent; 1- present.

23. Eye slits: 0- absent; 1- present.

These characters are used exactly as described by Edgecombe and Ramsköld (1999, character 5). Character 20 is inapplicable to taxa that do not possess eyes (Character 19, State 2).

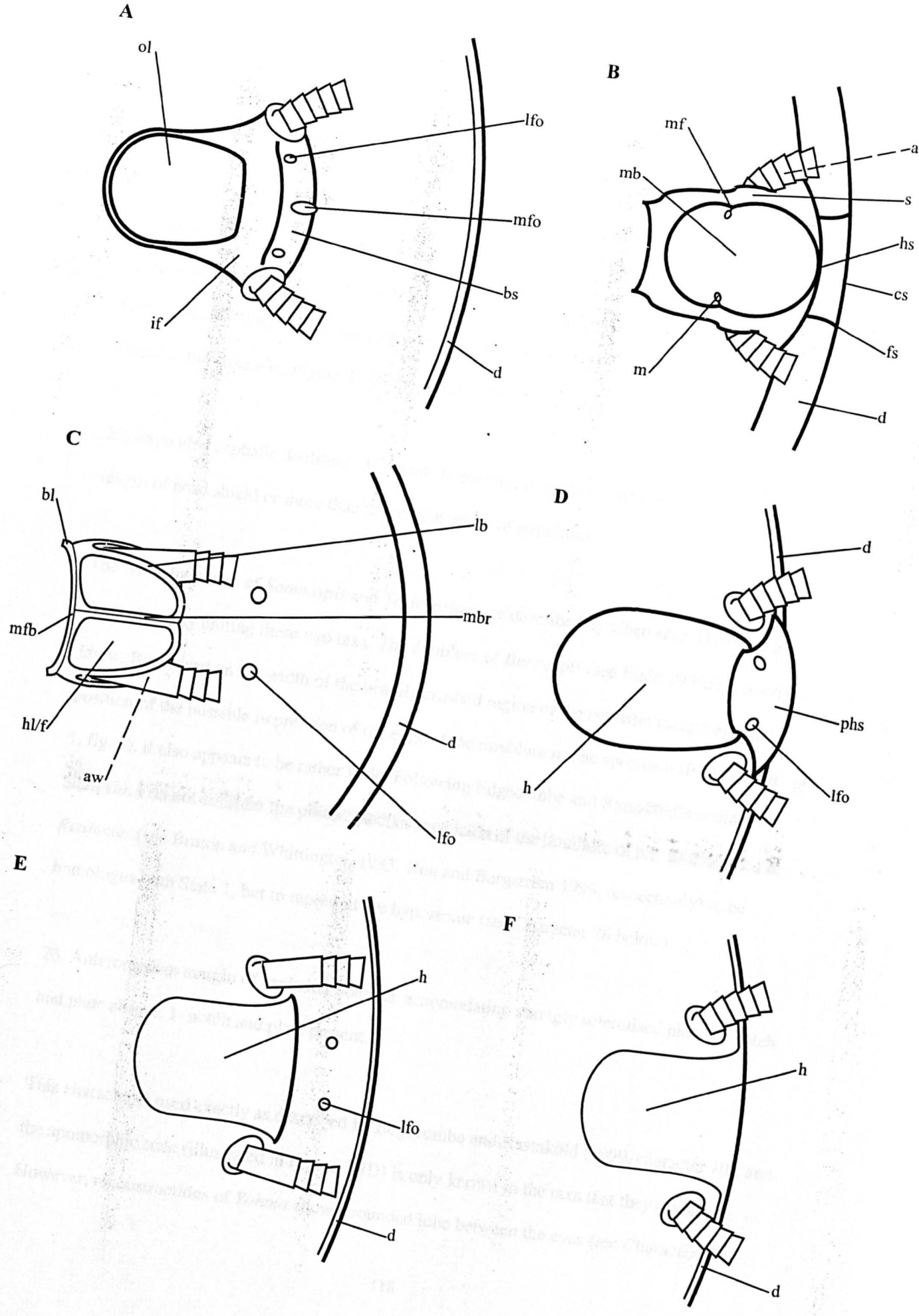
24. Dorsal median eyes: 0- absent; 1- present.

Dorsal median eyes on a tubercle are considered a synapomorphy of the Chelicerata (Dunlop and Selden 1997; Dunlop 1999). The nature and position of the structures interpreted as dorsal median eyes in *Mimetaster* (Stürmer and Bergström 1976, p. 82-84) are regarded as equivocal.

Ventral cephalic structures

Many characters of the ventral surface of the euarthropod head (see Figure 3.7) of potential phlyogenetic utility are poorly known in many important taxa. In particular, the presence of pre-hypostomal frontal organs (Figure 3.7A, C-E) is not coded herein (see Edgecombe and Ramsköld, 1999, p. 272). Definitive evidence of the absence of these structures is available for very few taxa, and the homology of these structures with the maculae of the trilobite hypostome (see Figure 3.7B

FIGURE 3.7. Ventral reconstructions of arachnomorph arthropod heads. A. *Misszhouia longicaudata*, after Chen *et al.* (1997), figs 2-4, 7; B. *Ceraurinella typa*, after Whittington (1992, pls 2, 5-6; 1997) and Chen *et al.* (1997, fig. 7); C. *Agnostus pisiformis*, after Müller and Walossek (1987); D. *Kuamaia lata*, after Edgecombe and Ramsköld (1999, figs 3.2, 5-6); E. *Cindarella eucala*, after Ramsköld *et al.* (1997).F. *Emeraldella brocki*, after Bruton and Whittington (1983). Not to Scale. Abbreviations: aw, anterior wing, beneath antennae; bs, boomerang-shaped sclerite; bl, blade-like process of posterior wing; d, doublure of head-shield; cs, connective suture; f, fenestra; fs, facial suture; h, hypostome; hl, hypostomal lobe (emerging through fenestrae of *Agnostus*); hs, hypostomal suture; if, intervening field of hypostomal complex; lb, lateral bridge; lfo, lateral frontal organ; mb, median body; mbr, median bridge; mf, median furrow; mfb, mouth field bridge; mfo. median frontal organ; ol, ovate lobe; phs, pre-hypostomal sclerite. Post-anternnal appendages and distal parts of antennae omitted.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and below) and the frontal organs of the crustacean labrum (e.g. see Müller and Walossek, 1987, p. 39) is uncertain. Secondly, the detailed homology of the trilobite hypostome with that of other putative arachnomorphs is unclear, and a very broad definition is consequently used herein. For example, various pre-hypostomal sclerites (see Figure 3.7A, D) in other arachnomorphs may have been incorporated, along with a primitive hypostome, into a single sclerite that is recognised as the hypostome in trilobites. The structure of the hypostome (e.g. the presence of paired anterior wings dorsal to the antennae, Figure 3.7B-C) may also be a source of additional characters.

25. Expanded cephalic doublure: 0- absent; 1- present, maximum width more than 30 percent length of head shield or more than 25 percent width of pygidium.

The wide doublures of *Soomaspis* and *Taricccoria* were described by Chen *et al.* (1996) as a synapomorphy uniting these two taxa. The doublure of *Buenaspis* (see Budd 1999*a*) is poorly know. But, based on the width of the heavily crushed region of the cephalic margin and the position of the possible impression of the edge of the doublure in one specimen (Budd *op. cit.*, pl. 1, fig. 1), it also appears to be rather wide. Following Edgecombe and Ramsköld's coding of *Sidneyia*, I do not consider the posteromedian expansion of the doublure of e.g. *Emeraldella* or *Retifacies* (see Bruton and Whittington 1983; Hou and Bergström 1999, respectively) to be homologus with State 1, but to represent the hypostome (see Character 26 below).

26. Anteromedian margin of cephalon notched, accomodating strongly sclerotised plate: 0- notch and plate absent; 1- notch and plate present.

This character is used exactly as described by Edgecombe and Rasmköld (1999, character 10), and the apomorphic state (illustrated in Figure 3.7D) is only known in the taxa that they discussed. However, reconstructions of *Yohoia* show a rounded lobe between the eyes (see Character 19)

anterior to, and distinct from, the head shield, which resembles the anterior sclerite recognised here. This seems to be a misinterpretation. Specimens preserved in dorsal aspect (USNM 57696, Whittington 1974, pl. 2, figs 1-3) and lateral aspect (USNM 57694, Whittington *op. cit.*, pl. 1, fig. 1; USNM 155616, pl. 5, fig. 2) clearly seem to show that this 'median lobe' is a downward curving, pointed, extension of the head shield.

27. Hypostomal sclerite: 0- median extension of the doublure, with no suture; 1- natant, sclerite not in contact with doublure; 2- with narrow overlap with pre-hypostomal sclerite; 3- narrow attachment to doublure at hypostomal suture; 4- absent.

The homology of hypostomes and labra has not previously been discussed in any detail. The euarthropod labrum is likely to represent a posteroventral extension of the pre-segmental acron (Scholtz 1997). Often this structure is sclerotised and covers the mouth ventrally. It is this sclerite that is here identified as the hypostome. This character is therefore considered absent in taxa lacking a sclerite covering the mouth, irrespective of the morphology and position of the labrum itself which at least partly covers the mouth in all euarthropods other than pycnogonids (see Edgecombe *et al.* 2000, p. 167). The 'fleshy labrum' of crustaceans does not appear to be sclerotised, and a hypostome is consequently considered to be absent. The many derived features of the crustacean labrum are not a good reason to consider it non-homologous with the hypostome-bearing strucutre of other arthropods, as Walossek and Müller (1990) argued.

In many taxa the mouth is covered by a posteromedian extension of the doublure which is here considered to represent the hypostome (e.g. *Emeraldella*, Figure 3.7F; *Aglaspis*, see Hesselbo 1992, fig. 5.2). In others, the hypostome is separated from the doublure by a suture, by a pre-hypostomal sclerite (e.g. *Kuamaia lata*, Figure 3.7D; *Saperion glumaceum*, see Edgecombe and Ramsköld 1999, figs 3-4) or by an intervening region of unsclerotised cuticle (the natant condition of Fortey 1990*b*, e.g. *Cindarella eucala*, Figure 3.7E). The homology of pre-hypostomal sclerites

and hypostomes in helmetiids, trilobites and naraoiids (see Figure 3.7) have been discussed by Chen *et al.* (1996) and Edgecombe and Ramsköld (1999), but it is as yet unclear if any of the character states described here are derived from any other. They are here treated as distinct, and the character as unordered, pending further study.

No hypostome has been identified in *Yohoia* (see above), *Alalcomenaeus*, *Jianfengia*, *Fortiforceps* or *Leanchoilia*, and there is certainly no broad posterior extension of the doublure in any of these taxa. Since there is also no pre-hypostomal sclerite, they have received a (134) partial uncertainty coding. The attachment of the hypostome of *Tegopelte* is unclear, but it would seem not to be attached to any doublure (Whittington 1985) and it is therefore given a (12) uncertainty coding.

The 'rostrum-like structure' on the ventral surface of *Lemoneites* appears to be similar in morphology and position relative to the anterior margin of the head shield (Flower 1968, pl. 8, figs 4, 13) to that described from *Aglaspis* and is coded as State 0. In many taxa the hypostome is unknown, but in only a small number can it reliably be coded as absent. Hughes (1975) suggestion that the hypostome of *Burgessia* is absent is preliminarily accepted, but an extension of the doublure may be visible in some of Hughes's figures. Fortey (pers. comm., 2000) also doubts Hughes's assertion.

28. Visible ecdysial sutures: 0- absent; 1- present.

The marginal ecdysial sutures of chelicerates and the dorsal sutures of trilobites are almost certainly not homologous, but the presence of sutures and their position (see Character 28, below) are coded separately to allow this to be tested. Marginal sutures were coded as present in *Sidneyia* by Wills *et al.* (1998*a*, character 2) following Bruton's (1981) suggestion, but this is considered equivocal here.

29. Position of ecdysial sutures: 0- marginal; 1- dorsal.

This character is inapplicable to taxa lacking ecdysial sutures (Character 28, State 0). Dorsal sutures, whilst present in the representatives of the Trilobita coded here, are probably not a synapomorphy of trilobites as a whole but for a clade of trilobites excluding the Olenellida (Whittington 1989; Fortey 1990*a*).

Exoskeletal tergites and thoracic tagmosis

30. Mineralised cuticle: 0- absent; 1- present.

Calcification of the exoskeleton is one of the most convincing synapomorphies of the Trilobita (Fortey and Whittington 1989; Ramsköld and Edgecombe 1991; Edgecombe and Ramsköld 1999, character 1). Cuticle mineralisation is also coded as present in aglaspidids following Briggs and Fortey (1982), who suggested that the aglaspidid exoskeleton was originally phosphatic. Other aglaspidid-like forms, including *Lemoneites* and *Paleomerus*, probably also had a mineralised cuticle, but Hou and Bergström (1997, p. 97) argue that in these cases it was likely to be calcareous. An undescribed Silurian aglaspidid may also have had an originally calcitic cuticle (Fortey and Theron 1994, p. 856). Due to the uncertainty about the chemical composition of the exoskeleton in these forms, cuticle mineralisation is coded as potentially homologous in all these taxa, and no attempt is made to code separate states for phosphatic and calcareous mineralisation.

31. Trunk tergites with expanded lateral pleurae covering appendages dorsally: 0- absent; 1- present.

Whilst the presence of paratergal folds may be a synapomorphy at the level of the Euarthropoda (Boudreaux 1979; Wägele 1993; Edgecombe *et al.* 2000, character 142, p. 185), these are at most small reflections of the margin of the tergites in most euarthropods. In arachnomorph taxa these are expanded to form large lateral pleurae that cover the appendages dorsally (see e.g. *Limulus* and *Triarthrus* in Boudreaux 1979). This is inferred to be the case in some taxa where dorsal features and appendages are poorly known, on the basis of their possession of tergites with wide pleural regions. This feature was suggested as typical of lamellipedians (= arachnomorphs) by Hou and Bergström (1997, p. 42-43).

The arrangment of the thorax of *Marrella*, *Mimetaster* and *Burgessia* differs from that of all the other taxa considered here in that the appendages seem to be attached to the lateral margins of the body. The trunk tergites (in *Burgessia* they are covered by a posterior extension of the head shield) do not cover the appendages and seem to entirely lack pleurae. This character has been clearly described in *Mimetaster* (Stürmer and Bergström 1976, pp. 87-90, fig. 8) and *Burgessia* (Hughes 1975, p. 421).

32. Free thoracic tergites: 0- present; 1- absent.

Following Edgecombe and Ramsköld (1999, character 16), a number of taxa lack functional post-cephalic articulations and consequently lack free thoracic tergites. Despite this, they code these taxa for a number of characters relating to the structure of thoracic tergites (e.g. their characters 18 and 19). These characters are here treated as inapplicable to taxa without free tergites and the definition of this character has been modified from that of Edgecombe and Ramsköld (1999) to make this more explicit.

33. Decoupling of thoracic tergites and segments: 0- absent; 1- present.

Ramsköld *et al.* (1997) described this unique character of *Cindarella* and *Xandarella*, where the thoracic tergites correspond to a variable, increasing posteriorly, number of appendage pairs. This character cannot be coded for taxa in which free thoracic tergites are absent (Character 31, State 1).

34. Tergite articulations: 0- tergites non-overlapping; 1- extensive overlap of tergites; 2- edge-to-edge pleural articulations.

In most of the taxa considered here, the thoracic tergites overlap considerably and relatively evenly over their width. This contrasts with the primitive euarthropod condition, where the tergites do not overlap medially, as seen in stem-group crustaceans. In trilobites, *Helmetia* and *Kuamaia* (see Edgecombe and Ramsköld 1999, character 18), overlap of thoracic tergites is limited to a well-defined axial region, and the lateral pleurae meet edge-to-edge.

The thoracic articulations of naraoiids with free thoracic tergites are in some ways similar to those of trilobites, with a strong overlap medially that is lacking abaxially, and anterolateral articulating facets (Ramsköld and Edgecombe 1999; Budd 1999*a*). However, the distribution of these features in other trilobite-like arachnomorphs is unclear, and here a restrictive coding is used. I do not consider that this character can reliably be applied to the fused thoracic tergites of *Saperion*, *Tegopelte* and *Skioldia*, and this character is coded as inapplicable to all taxa lacking free thoracic tergites (Character 31, State 1).

35. Trunk effacement: 0- trunk with defined (separate or fused) tergite boundaries; 1- trunk tergite boundaries effaced laterally; 2- trunk tergite boundaries completely effaced.

The distribution of tergite boundary effacement was discussed by Edgecombe and Ramsköld (1999, p. 273, character 15). Contrary to Edgecombe and Ramsköld, I consider *Skioldia* and

Saperion to show a distinct form of tergite effacement, where the fused tergite boundaries are defined by furrows axially but effaced laterally. The boundaries are at least effaced laterally in *Tegopelte*, but the axial region of the exoskeleton is unknown, which accordingly is given a multistate uncertainly coding.

36. Cephalic articulation fused: 0- absent; 1- present.

Uniquely in *Tegopelte*, *Saperion* and *Skioldia* the articulation of the head with the thorax is non-functional, and the entire exoskeleton forms a single tergite.

37. Head shield overlap of thoracic tergites: 0- overlap absent or identical to overlap between thoracic segments; 1- head shield covers first thoracic tergite only; 2- head shield covers mutliple anterior trunk tergites.

38. Head shield articulates with reduced anterior thoracic tergire: 0- absent; 1- present.

Amongst taxa showing a posteriorly expanded head shield i.e. one that overlaps the thorax, Edgecombe and Ramsköld (1999, character 9) identified two distinct character states. One of these, overlap of only the anteriormost thoracic tergite, was limited to taxa assigned to the Liwiinae (*sensu* Fortey and Theron 1994), another, overlap of multiple tergites with attachment to a reduced anterior thoracic tergite, to the Xandarellida. None of the additional taxa considered herein (including *Buenaspis*, which was assigned to the Liwiinae by Budd 1999*a*) show these distinctive morphological features. However, the expanded head shields of *Marella*, *Mimetaster* and *Burgessia*, which do not articulate with a narrow anterior thoracic tergite, may be homologous with the expanded head shields of xandarellids. To recognise this the degree of overlapping of the thorax and the possession of the reduced anterior tergite are coded separately. These characters are

both coded as inapplicable to taxa in which the head shield and thoracic tergites are fused (Character 35, State 1). The crustacean carapace, which is most similar to the head shield of *Burgessia*, is seemingly absent in stem-group taxa (Walossek and Müller, 1998).

39. Trunk narrowed anteriorly relative to head shield, widest posteriorly: 0- absent; 1- present.

This character is used here as described by Edgecombe and Ramsköld (1999, character 14). The anterior narrowing of the trunk caused by the reduction of opisthosomal segment 1 in xiphosurids (*Weinbergina*, of the taxa analysed here see Andersen and Selden 1997; Dunlop and Selden 1997, character 14) is not considered to be homologous with the unusual shape of the thorax in naraoiids recognised by their coding.

40. Boundaries of anterior trunk segments reflexed anterolaterally: 0- absent, boundaries transverse or reflexed posterolaterally; 1- present.

41. Joints between posterior tergites functional, anterior ones variably fused: 0- absent; 1- present.

42. Posterior tergite bearing axial spine: 0- absent; 1- present.

These three characters are coded following Edgecombe and Ramsköld (1999, characters 17, 19 and 23). In addition to the taxa considered here, a thoracic axial spine is present in some olenelloid trilobites (see Lieberman 1997, characters 73 and 74) and in the aglaspidid *Beckwithia* (see Hesselbo, 1989).

Body termination

43. Postabdomen of segments lacking appendages: 0- absent; 1- present.

44. Length of postabdomen: 0- 1 segment; 1- 2 segments; 2- 3 segments; 3- 5 segments.

In some taxa, a variable number of posterior thoracic segments bear complete tubular tergites and lack appendages. In *Aglaspis*, autapomorphically, it seems that the posterior three thoracic segments lack appendages (Briggs *et al.* 1979; Hesselbo 1992) but have unmodified tergites. These situations are recognised as potentially homologous by the coding used here. Character 43 is coded as inapplicable to taxa lacking a postabdomen.

45. Posterior tergites strongly curved in dorsal aspect compared to anterior tergites: 0- absent; 1- present.

As recognised by Wills *et al.* (1998*a*, character 17), the curvature of thoracic tergites, in some taxa where the tergites are distinct, increases posteriorly so that the posterior tergites are highly curved to semicircular in dorsal aspect. This situation is not known from crustaceans or from stem-group arthropods.

46. Posterior segments reduced and with highly reduced appendages: 0- present; 1- absent.

In some taxa, there are a large number of posterior segments that are sagitally short and have appendages that are much reduced in size compared to anterior trunk appendages. These somites are incorporated into the pygidium in some taxa, but primitively they are covered by tiny free trunk tergites. In the derived state, the trunk somites and limbs are of a relatively constant size. The

distinction between these states can be seen when an attempt is made to count the number of segments that make up the body. In taxa showing State 0, the number of segments is very high and difficult to count, whereas in other taxa, the number of post-cephalic segments is easily assessed.

47. Pygidium: 0- absent; 1- present.

A pygidium is recognised here as a posterior tagma consisting of a number of fused segments under a single tergite, which may or may not incorporate the post-segmental telson. This is different to the use of this term by Edgecombe and Ramsköld (1999), which follows Ramsköld *et al.* (1997), and very different to its use by Wills *et al.* (1998*a*, p. 53) as a synapomorphy of the Trilobita. My definition recognises the situation in *Retifacies*, where the spinose postsegmental telson is autapomorphically not fused to the pygidium, as homologous to other multisegmented posterior tagma which include the telson. The distinction between the pygidium and an expanded post-segmental telson can also be seen in the position of the anus, which amongst putative arachnomorphs is consistently in the posteriormost pre-telsonic segment (see below). In taxa with a pygidium the anal segment is fused into the pygidium (see e.g. *Kuamaia*, Edgecombe and Ramsköld 1999, fig. 6), whereas in those taxa lacking a pygidium, the anus is between the final trunk tergite and the telson.

Ramsköld *et al.* (1997) argued that the posteriormost tergite of xandarellids (which incorporates the anal segment) is not homologous to the posterior tagma recognised as pygidia herein, because posterior thoracic tergites also cover multiple segments in xandarellids (see Character 32). Evidence of segmentation of the pygidium in a variety of taxa suggests that the number of segmental tergites fused to form the pygidium is greater than the number of appendages. For example, the pygidium of *Kuamaia* has two pairs of lateral spines but at least four pairs of appendages (Hou and Bergström 1997; Edgecombe and Ramsköld 1999) and that of *Triarthrus* only five axial rings posterior to the articulating ring but more than ten pairs of

appendages (Whittington and Almond 1987). The fact that decoupling of tergites and segments is evident in the thorax of *Xandarella* and *Cindarella* does not necessarily suggest that a similar decoupling, which is more widespread, in pygidia is the result of a different developmental process and hence non-homologous. Instead, the situation in the xandarellid thorax is potentially homologous to that found (more widely) in pygidia and consequently the terminal xandarellid tergite is a pygidium. It is unclear if decoupling of tergites and somites is primitively limited to the terminal tergite or primitively a property of the arachnomorph post-cephalon as a whole.

It has been suggested that the tiny pygidium of olenelloid trilobites, which probably best relfects the primitive trilobite state, consists only of the post-segmental telson (Harrington *in* Moore 1959) and is therefore not a true pygidium. However, Whittington (1989) has shown that the olenelloid pygidium consists of at least two and possibly as many as five or six segments and is therefore likely to be homologous with the pygidium of other trilobites.

48. Position of the anus: 0- terminal, within telson; 1- at base of telson.

In crustaceans and stem-group arthropods, the anus is terminal or otherwise situated in the telson (e.g. *Rehbachiella*, Walossek 1993, fig. 15D). In putative arachnomorphs, the anus is either at the junction of the posteriormost thoracic segment and the telson, or ventral within a fused pygidium. In the case of taxa with a pygidium, the anus is anterior to the posterior margin and, where known, positioned between the posteriormost pair of appendages, suggesting that it is anterior to the post-segmental telson (see e.g. *Olenoides*, Whittington 1980*b*).

49. Pygidium with median keel: 0- absent; 1- present.

Edgecombe and Ramsköld (1999, character 21) considered the presence of a median keel on the pygidium as a synapomorphy uniting *Soomaspis* and *Tarricoia*. They did not explain how this

structure can be distinguished from the raised pygidial axis of trilobites. Homology of these structures is not supported here, because the axis of more primitive trilobites (including *Eoredlichia*) is morphologically quite distinct from the naraoiid keel. Budd (1999*a*) noted the presence of a keel on the pyidium of *Buenaspis* and suggested (*op. cit.*, p. 102) that it may be an artefact of dorsoventral compaction. However, contrary to the coding of Edgecombe and Ramsköld (1999), a keel is clearly visible on pygidia of *Liwia convexa* (Dzik and Lendzion 1988, fig. 4c-d) which are preserved in full relief. It therefore seems unlikely that the keel is a taphonomic artefact. This character and the two following characters are not applicable to taxa lacking a pygidium (Character 46, State 0).

50. Pygidium with broad-based median spine: 0- absent; 1- present.

51. Pygidium with lateral spines: 0- present; 1- absent.

Edgecombe and Ramsköld (1999, character 22) coded the presence of a median spine and two pairs of lateral spines as potentially homologous in *Sinoburius*, *Kuamaia* and *Helmetia*. The distribution of lateral spines is much wider than that of terminal spines and they are therefore coded separately here. In trilobites, it has widely been recognised that lateral spines represent the original segmentation of the pygidium. This cannot be the case for median spines.

52. Expanded post-segmental telson: 0- absent; 1- present.

In a range of taxa, the posteriormost tergite is a large (relative to the thoracic tergites) structure that lacks any evidence of segmentation and is interpreted as representing an expanded tergite of the post-segmental telson, from which segments are released anteriorly during ontogeny. The posteriormost tergite of *Marrella* and probably *Mimetaster*, on the other hand, is small compared

to the thoracic tergites and rounded. This element probably represents the plesiomorphic euarthropod telson. The homology of this character in most taxa is clear, and only doubtful in *Retifacies*, in which it may be segmented. The figures of Hou and Bergström (1997) provide little unequivocal evidence for a telson in *Retifacies*, but the presence of this structure is very clear in colour photographs (e.g. Chen *et al.* 1996, fig. 198A). These figures, however, do not convincingly demonstrate the segmentation of the telson. *Retifacies* is interpreted here as being unique in possessing both a pygidium and an expanded post-segmental telson.

53. Telson shape: 0- spinose; 1- paddle-shaped.

The shape of the expanded telsons identified above varies from broadly spinose to flattened and paddle-like. This difference can be recognised both on the basis of the ratio of length to basal width (spinose telsons are relatively long) and by the change in width posteriorly (spinose telsons reduce in width posteriorly, paddle-shaped telsons increase in width). In eurypterids, a wide range of telson shapes is found, including both character states described here. It is likely that the plesiomorphic condition is a spinose telson. This character is inapplicable to taxa lacking an expanded telson.

54. Post-ventral furcae: 0- absent; 1- present.

This character recognises the potential homology of unsegmented, paired structures that articulate with the segment immediately anterior to the telson. The potential homology of these structures (the postventral plates) in *Emeraldella* and *Aglaspis* was recognised by Wills *et al.* (1998*a*, character 70), and in *Emeraldella* and *Sidneyia* by Edgecombe and Ramsköld (1999, character 25). The homology of the segmented pygidial caudal furcae of *Olenoides* (see Whittington 1975*a*, 1980*b*) with these structures is considered doubtful, and coded as equivocal.

Despite their distinctive morphology the long caudual furcae of *Cheloniellon* may be homologous with the furcae of *Aglaspis*, *Emeraldella* and *Sidneyia*. This is supported by the caudal furcae of the Ordovician cheloniellid *Duslia*, which are more similar in morphology to those of *Emeraldella* than of*Cheloniellon*. Chlupáč (1988, p. 614-616) considered these structures to be on the terminal tergite in *Duslia*. However, a feint tergite boundary is apparent posterior to the attachment of the furcae (see Chlupáč 1988, pl. 57, fig. 4), and they are therefore considered here to be attached to the pre-telsonic segment, as in *Cheloniellon*. Chlupáč (1988) and Dunlop and Selden (1997) supported a close relationship between *Duslia* and *Cheloniellon*.

Methods

All analyses were carried out using PAUP* version 4.0b4a (Swofford 1999) and, unless otherwise stated, used heuristic searches with 1000 random addition sequence replicates. The software packages MacClade version 3.07 (Maddison and Maddison 1997) and RadCon (Thorley and Page 2000) were used for comparing trees and investigating patterns of character evolution. Tree length and other statistics (the Consistency Index, C.I., and Retention Index, R.I.) were calculated by PAUP* and MacClade with uninformative characters excluded. Analyses were run separately using each of the different codings for aglaspidids.

Characters were treated as unordered and of equal weight in most analyses. To assess the influence of this assumption, four of the eight multistate characters, which have states that are intermediate between others (Wilkinson 1992), were treated as ordered in some analyses. These characters are the number of cephalic segments (Character 4), the length of raptorial appendage spines (Character 6), the degree of overlap of the thorax by the head-shield (Character 37) and the number of segments making up the postabdomen (Character 44). The last of these is uninformative when not ordered, because only one taxon shows each of states 0, 1 and 3.

Support for individual nodes was assessed by bootstrap analysis (Felsenstein 1985) and by calculating Bremer support indices (Bremer 1988, 1994). These methods measure two distinct aspects of support for phylogenetic hypotheses. Trees or nodes may be considered well supported (1) to the extent to which alternative topologies are much less parsimonious, as measured by the support index (Wilkinson 1996), or (2) where they are consistent with a large proportion of characters, so that character sampling is unlikely to have had much influence on topology, as assessed by bootstrapping (Page 1996). Bootstrapping was performed with 100 bootstrap replicates, each of ten addition sequence replicates. Bremer support indices are based on heuristic searches with 100 addition sequence replicates.

Three pairs of terminals are included in Table 6 that, apart from missing data, are coded identically. These are *Helmetia* and *Kuamaia*, *Soomaspis* and *Taricoia*, and *Saperion* and *Skioldia*. These pairs are 'taxonomically equivalent' and must appear as sister taxa in any cladistic analysis. They can be recoded as single terminals according to the principal of safe taxonomic reduction (Wilkinson 1995) and were not considered separately in the analyses presented here. Cladistic analyses were therefore carried out on the basis of 33 terminals. Edgecombe and Ramsköld (1999) ignored this problem, but coded the same three pairs of taxa and *Eoredlichia* and *Chuaria* identically for their more limited set of characters.

Results

Analysis with all characters unordered and using the 'Aglaspidida 1' coding found nine most parsimonious trees (MPTs), each 126 steps long (C.I. = 0.556, R.I. = 0.763). Using the 'Aglaspidida 2' coding resulted in 18 MPTs of length 125 (C.I. = 0.560, R.I. = 0.765). Nine of these trees were those found with the first coding of aglaspidids. The strict component consensus (*sensu* Wilkinson 1994) of all 27 trees is shown in Figure 3.8. All trees supported the monophyly

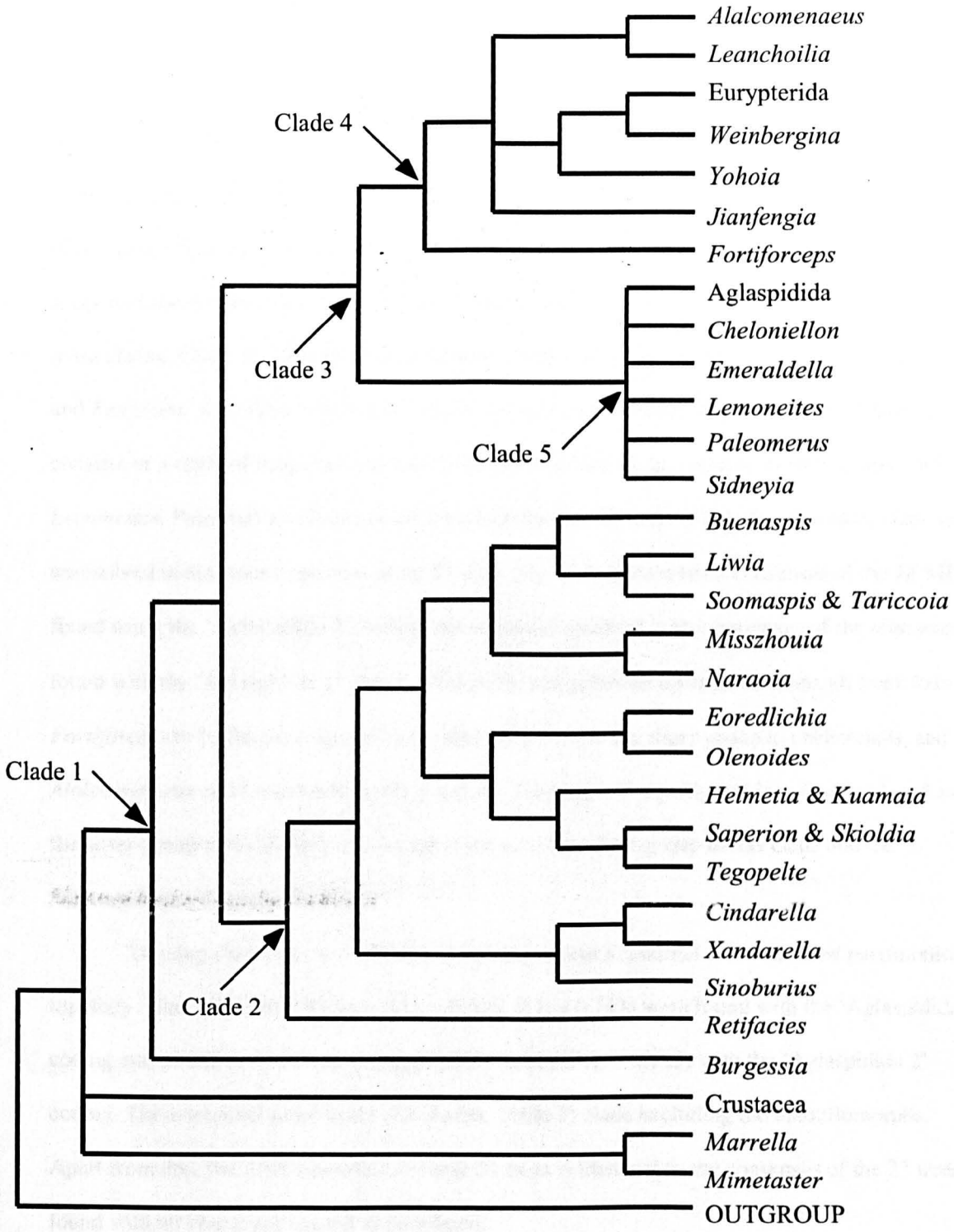


FIGURE 3.8. Strict consensus of 27 MPTs from four separate analyses of arachnomorph phylogeny, with different interpretations of aglaspidid morphology and with some characters treated as ordered or all characters unordered. Clades referred to in the text are numbered.

of the Marrellomorpha (*Marrella* and *Mimetaster*) and of a clade including all other taxa except Crustacea (Clade 1 of Fig. 3.8). The relationships between these two clades and the Crustacea were unresolved, equal numbers of trees in both analyses supported each of the topologies (Clade 1 (Crustacea, Marellomorpha)), (Crustacea (Marellomorpha, Clade 1)) and (Marellomorpha (Crustacea, Clade 1)). All trees placed *Burgessia* as the sister-taxon to the rest of Clade 1 and supported the division of the rest of Clade 1 into two major sister-clades. The topology of one of these clades (Clade 2), which included trilobites, helmetiids, tegopeltids, naraoiids, xandarellids and *Retifacies*, was stable with respect to the coding of aglaspidids. The other clade (Clade 3) consists of a clade of megacheirans and chelicerates (Clade 4), and a clade including aglaspidids, *Lemoneites*, *Paleomerus*, *Cheloniellon*, *Emeraldella* and *Sidneyia* (Clade 5). This latter clade is unresolved in the strict consensus of all 27 trees (Fig. 3.8) and the strict consensus of the 18 MPTs found using the 'Aglaspidida 2' coding, but was fully resolved in the consensus of the nine trees found with the 'Aglaspidida 1' coding. Within the megacheiran-chelicerate clade, all trees found *Fortiforceps* to be the sister-group to all other taxa, *Yohoia* the sister-group to chelicerates, and *Alalcomenaeus* and *Leanchoilia* to form a clade. *Jianfengia* is equally parsimoniously placed as the sister-group to the *Yohoia*-chelicerate clade or as the sister-group to this clade and the *Alalcomenaeus-Leanchoilia* clade.

Treating characters 4, 6, 37 and 44 as ordered had a minimal effect on most parsimonious topology. Nine MPTs of 136 steps (C.I. = 0.515, R.I. = 0.743) were found with the 'Aglaspidida 1' coding and 12 MPTs 135 steps in length (C.I. = 0.519, R.I. = 0.745) with the 'Aglaspidida 2' coding. These trees all supported a (Crustacea, Clade 1) clade excluding the marrellomorphs. Apart from this, the strict consensus of these 21 trees is identical to the consensus of the 27 trees found with all characters treated as unordered.

Across all analyses, four different topologies for Clade 5 (of Fig. 3.8) were found, as shown in Figure 3.9. The distribution of these topologies across the four analyses described above, and across the same analyses repeated after reweighting of each character in proportion to their

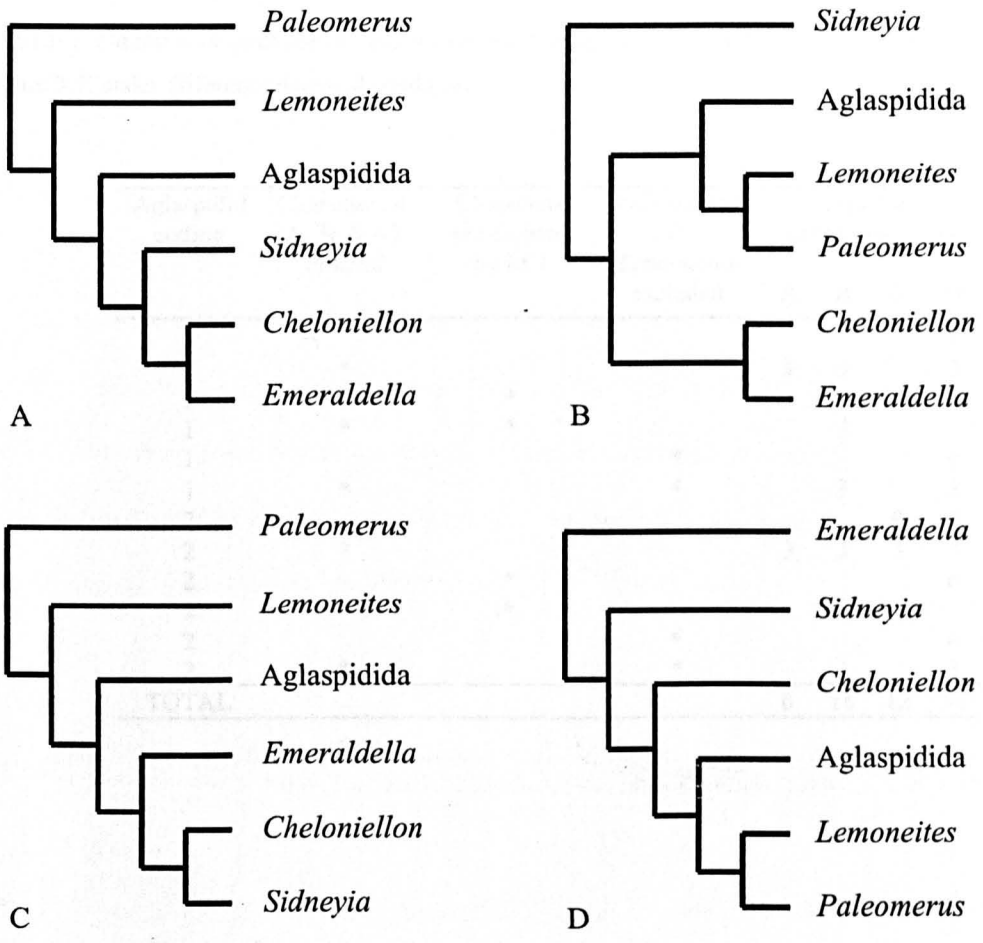


FIGURE 3.9. Alternative equally parsimonious resolutions of Clade 4 of Figure 3.8. See Table 7.

TABLE 7. Numbers of most parsimonious trees supporting each of the alternative topologies for Clade 4 of Figure 3.7, under different analytical conditions.

Aglaspidid coding	Characters 4, 6, 36 & 43 ordered	Characters reweighted by RCI	*Paleomerus* & *Lemoneites* excluded	Topology (see Figure 3.8)			
				A	B	C	D
1							9
1	*			3	3		3
1		*					6
1	*	*			3		
1			*				6
1	*		*		3		3
2						9	9
2	*			3	3	3	3
2		*					6
2	*	*			3		
2			*				6
2	*		*		3		3
TOTAL				6	18	12	54

Rescaled Consistency Index (see Farris 1989) from the first analysis is shown in Table 7. The instability of this clade was to some extent due to the inclusion of *Lemoneites* and *Paleomerus*, which could each be coded for only 27 of the 54 characters used. Analysis with these two taxa excluded and characters treated as unordered found trees compatible only with Topology D of Figure 3.9, irrespective of the coding used for aglaspidids. Analysis with some characters treated as ordered and using either aglaspidid coding found three trees compatible only with Topology B of Figure 3.9 and three compatible only with Topology D of Fig. 3.9. Toplogy D is therefore the preferred topology for Clade 5, as shown in Table 7.

One of the MPTs that was found with the 'Aglaspidida 2' coding and all characters treated as unordered was chosen as the basis for further discussion. This tree combined the preferred topology of Clade 5 with the (Crustacea, Clade 1) group that was favoured when some characters were treated as ordered. Bootstrap percentages and Bremer support values for this tree (using the Aglaspidida 2 coding) are shown in Figure 3.10. Apomorphies for all ingroup nodes of this tree are also shown in Figure 3.10.

DISCUSSION OF PHYLOGENETIC RESULTS

The results of the cladistic analyses presented above are well resolved and robust with respect to different analytical parameters. Most of the taxa considered form a clade (Clade 1 of Figure 3.8) that is more closely related to chelicerates than to crustaceans in all analyses and is therefore recognised as the Arachnomorpha, as defined by Chen *et al.* (1996) and Ramskold *et al.* (1996). The monophyly of the Marrellomorpha was supported in all analyses. The marrellomorphs were found to be the sister-group to a Crustacea + Clade 1 group in most MPTs, but in a minority of trees formed the sister-group to Clade 1 alone. According to the latter result, they should be included within the Arachnomorpha but according to the first, excluded from it. Both of these

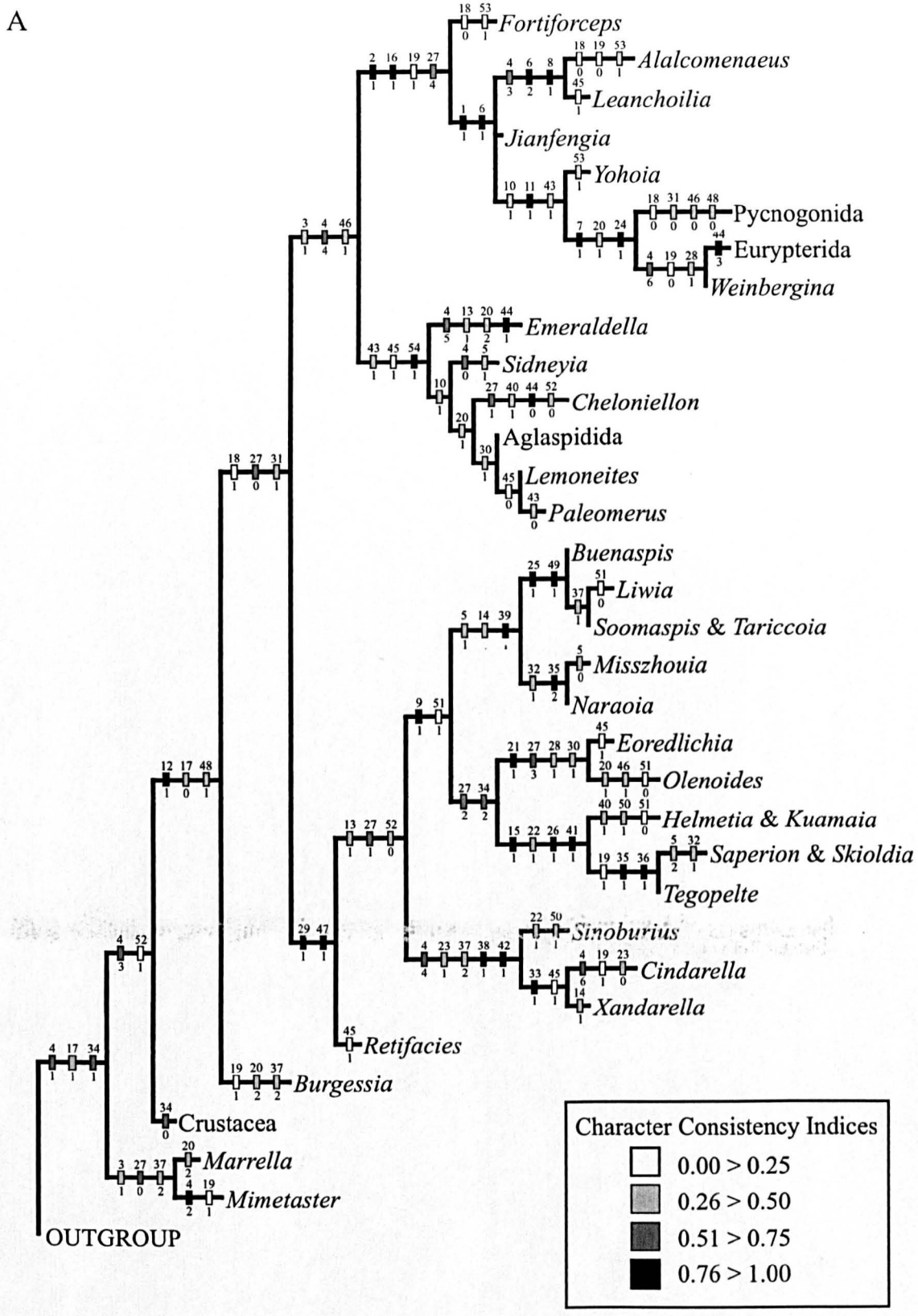
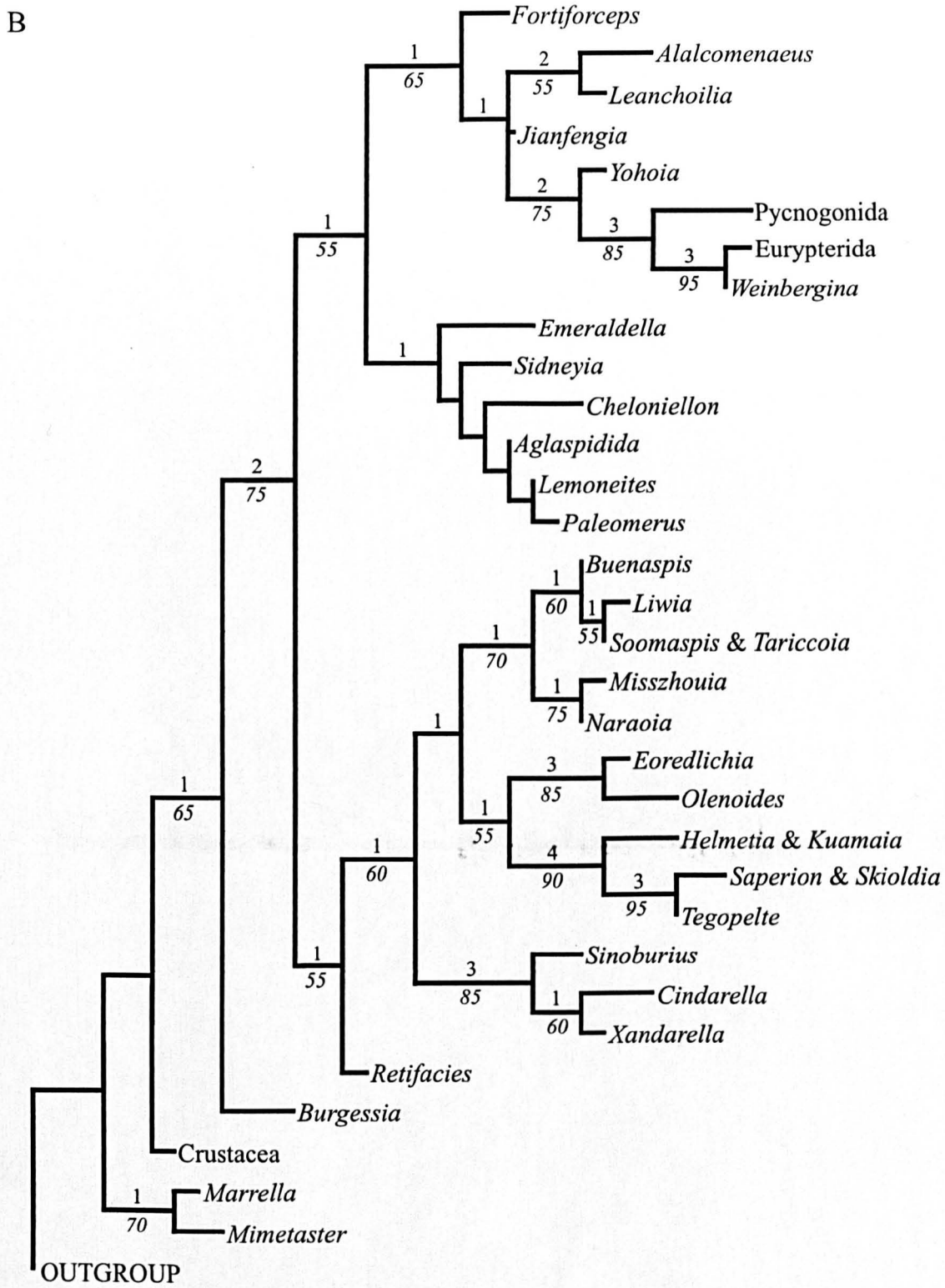


FIGURE 3.10. One of 18 equally parsimonious cladograms with 'Aglaspidida 2' coding and all characters unordered that is most congruent with results from other analyses. Non-terminal branch lengths scaled to reflect number of apomorphies. A. Showing ACCTRAN apomorphy scheme. Character numbers, above boxes, and character states, below boxes, as in Table 7 and text. Character consistency indices indicated by shading. B. Showing levels of support for individual nodes. Bremer support indices are shown in bold type above branches. Bootstrap percentages are shown in italic type below branches, for all nodes with relative frequencies greater than 50 per cent.


B
Fortiforceps
Alalcomenaeus
Leanchoilia
Jianfengia
Yohoia
Pycnogonida
Eurypterida
Weinbergina
Emeraldella
Sidneyia
Cheloniellon
Aglaspidida
Lemoneites
Paleomerus
Buenaspis
Liwia
Soomaspis & Taricoia
Misszhouia
Naraoia
Eoredlichia
Olenoides
Helmetia & Kuamaia
Saperion & Skioldia
Tegopelte
Sinoburius
Cindarella
Xandarella
Retifacies
Burgessia
Crustacea
Marrella
Mimetaster
OUTGROUP

alternatives have been supported in previous studies (e.g. Hou and Bergström, 1997; Wills *et al.*, 1998*a*, respectively). In addition to the marrellomorphs, the Fuxianhuiida Bousfield, 1995 and Canadaspidida have been placed in the Euarthropoda outside the main mandibulate and arachnomorph clades (Hou and Bergström, 1997). Further study of these taxa, of the crustacean, or mandibulate, stem-group and of the marrellomorphs is necessary before the position of the Marrellomorpha can be resolved. Provisionally, marrellomorphs are excluded from the Arachnomorpha, following the majority of analyses above and Wills *et al.* (1994).

The Burgess Shale arthropod *Burgessia* was placed as the sister-group to remaining arachnomorphs in all analyses. Other Arachnomorpha form two major clades, one consisting of the 'trilobite-allied' arachnates analysed by Edgecombe and Ramsköld (1999), the other ('chelicerate-allied') clade including chelicerates, 'great appendage' arthropods, aglaspidids, *Lemoneites*, *Paleomerus*, *Sidneyia* and *Emeraldella*. The topology of the 'trilobite-allied' clade was similar to that found by Edgecombe and Ramsköld (*op. cit.*) but our results are more completely resolved, unambiguously supporting the sister-group relationship between trilobites and Helmetiida suggested in the previous study.

Within the 'chelicerate-allied' clade, Aglaspidids, *Paleomerus*, *Lemoneites* and the Burgess Shale *Emeraldella* and *Sidneyia* form a clade in opposition to megacheirans and chelicerates. A close relationship between *Lemoneites* and chelicerates, as suggested by Flower (1968) and Dunlop and Selden (1997), is not supported. Rather, *Lemoneites* is most parsimoniously considered a derived aglaspidid that is convergent with chelicerates in possessing a postabdomen. Our analysis provides strong support for a new hypothesis of the origin of the chelicerates from within a paraphyletic assemblage of megacheiran arthropods. Previous hypotheses of the chelicerate sister-group (see above) are much less parsimonious. The shortest trees supporting a *Cheloniellon*-chelicerate clade are six steps longer than the MPTs and those supporting an aglaspidid-chelicerate clade seven steps longer. All megacheirans and chelicerates are united by the flap-shaped rounded exopods and modification of the second cephalic segment

endopods into anteriorly directed spinose raptorial organs, which share a number of detailed similarities. A clade including all of these taxa apart from *Fortiforceps* is supported by the synapomorphic loss of the antennae (or antennulae of crustaceans) and the longer length of spinose projections of the second cephalic appendage endopods. Within this clade, *Yohoia* shares the loss of cephalic exopods, the loss of thoracic endopods and a postabdomen of tubular tergites with chelicerates.

The poor resolution of Clade 5 (of Fig. 3.8) was partly due to the poor preservation of, and consequent high proportion of missing data for, *Lemoneites* and *Paleomerus*. When these two taxa were excluded from the analyses, only two (B and D) of the four topologies found in the complete analysis remained most parsimonious (see Fig. 3.9 and Table 7). Secondly, Bremer support values throughout much of the 'chelicerate-allied' clade (Clade 3 of Fig. 3.8) were improved when these taxa were excluded (see Fig. 3.11).

Dunlop (1999, p. 258) suggested that in reconstructing the chelicerate stem lineage 'we might predict that the two most significant changes towards the chelicerate condition are the reduction of the antennae and the formation of the next appendages into a claw'. According to the hypothesis presented here, both of these adaptations were achieved in Early Cambrian chelicerate ancestors. The recognition of the loss of the antennae in the stem-group of the chelicerates and the phylogenetic hypothesis presented here, suggest that chelicerates are most closely related to taxa with only a single additional segment fused to the crown-group euchelicerate head of four fused somites. Previous hypotheses have derived chelicerates from Palaeozoic arthropods with a longer head (e.g. *Cheloniellon*, Stürmer and Bergström 1978; *Sanctacaris*, Briggs and Collins 1988; *Emeraldella*, Bruton and Whittington 1983). The plesiomorphic pattern of head segmentation is matched in pycnogonids, in which only the anterior four pairs of appendages are incorporated into the head (e.g. Begström *et al.* 1980). This supports the view that pycnogonids are primitive with respect to other chelicerates, which show more-or-less complete fusion of this primitive head and three thoracic segments, including Solifugida and Pseudoscorpionida.

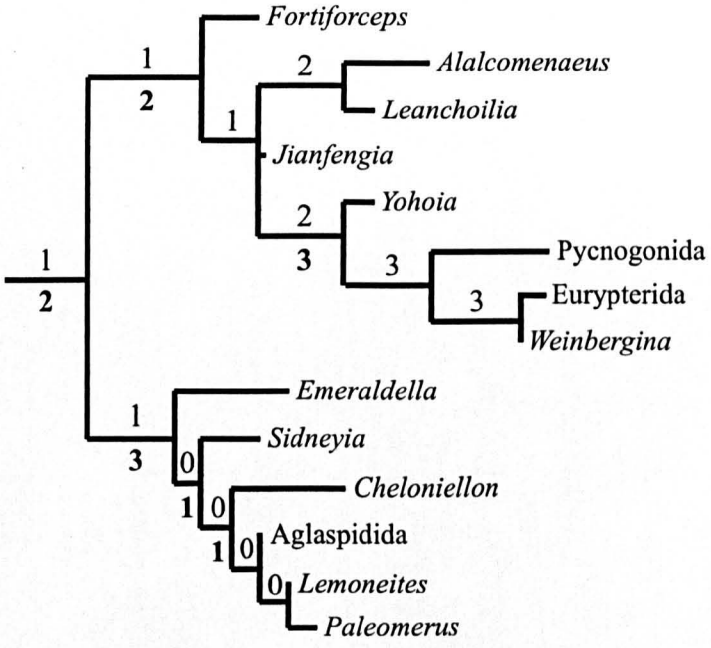


FIGURE 3.11. Bremer support values for clades within the 'chelicerate-allied' arachnomorphs (Clade 3 of Figure 3.8) when all taxa were included (normal weight font above nodes) and with *Lemoneites* and *Paleomerus* excluded (bold type below nodes).

This study suggests that a shift from gnathobasic benthic feeding to a more vagrant lifestyle and raptorial appendage feeding occurred very early in the chelicerate lineage. Appendage feeding was clearly an important adaptation for the terrestrialization of chelicerates (Dunlop, 1997, p. 69; Dunlop and Webster, 1999) but the model proposed here suggests that this considerably pre-dated terrestrialization. Gnathobasic feeding in xiphosurans and eurypterids may represent a reversal to a more primitve benthic arachnomorph lifestyle from a more pycnogonid-like ancestor.

MORPHOLOGICAL EVOLUTION OF ARACHNOMORPHS

The extant arthropod classes show highly conserved patterns of head segmentation (e. g. Wills *et al.*, 1994). In contrast, there has been a near consensus amongst Cambrian arthropod workers (although rarely based on anything resembling an explicit phylogenetic hypothesis) that patterns of head segmentation are highly homoplastic and hence of little systematic significance. Stürmer and Bergström (1978, p. 78-79) suggested that 'even closely related forms may have different numbers of head segments and appendages', Bruton and Whittington (1983, p. 576-577) that 'discussion on fossil arthropod relationships based on head segmentation... appears to be largely irrelevant and, at best, speculative' and Delle Cave and Simonetta (1991, p. 191) that 'there are no obvious phyletic affinities between genera having the same number of cephalized segments'. Most recently, Bergström and Hou (1997, p. 104) concluded that 'the segmental length of the head shield... seems to be of no relevance to the discussion and discrimination of evolutionary lineages'. It has been claimed that this view is supported by cladistic analyses in which patterns of tagmosis have been found to be rather poor at defining major arthropod clades (Briggs *et al.* 1992*a*, Wills *et al.* 1994).

This suggestion is not only of relevance to systematics, but has featured prominently in recent debates surrounding the nature of the 'Cambrian explosion' (see e.g. Budd and Jensen 2000, for a recent review). Gould (1989, 1991) argued that the apparent plasticity of head segmentation

in Cambrian compared to post-Cambrian arthropod evolution suggest that body-plan evolution was only constrained after the Cambrian explosion. According to this view, the origin of new higher taxa, with distinct body-plans, was only possible before the onset of these constraints (e.g. Valentine 1995). Taxa here recognised as arachnomorphs clearly played a major role in the development of Gould's hypothesis. This suggestion has previously been assessed in terms of overall morphological diversity, which is clearly rather distinct from Gould's concept of disparity. Wills *et al.* (1998*b*) showed that there was little correlation between overall morphological disparity and degree of limb specialization and that the latter was phylogenetically highly plastic. They remarked that (*op. cit.*, p. 64) 'this finding has important implications for models of arthropod phylogeny and evolution that attribute overiding importance to head segmentation', but did not explicitly examine head segmentation, although it is likely to have been a major component of the index of tagmosis employed.

The results of this study suggest that arguments that arthropod head segmentation was unusually labile during the Cambrian are poorly founded. Rather, only four major patterns of euarthropod head segmentation are identified. The plesiomorphic euarthropod state, according to both Walossek and Müller (1997, 1998) and Scholtz (1997), which may more properly be the plesiomorphic state for the euarthropod crown-group only (depending on the phylogenetic position of the Marrellomorpha), consists of four post-acronal segments, bearing the antennae and three pairs of biramous limbs. I propose that the term 'cephalon' be restricted to this kind of head, which is found in stem-group mandibulates. Crown-group mandibulates share a 'bimaxillary head', in which an additional pair of appendages, the labium or second maxillae, are incorporated into the head, but in crustaceans are not fused to the carapace (Scholtz 1997). Finally, two distinct forms of head tagmosis are found in chelicerates. A head with four pairs of appendages (but without antennae, giving a total of five segments incorporated into the head), which has been called the 'cephalosoma', is present in pycnogonids and in some euchelicerates. The 'prosoma' of euchelicerates consists of this cephalosoma and two additional segments.

These patterns of head segmentation are, in general, highly phylogenetically conserved (see Figure 3.12). Only three homoplastic changes, namely reversal to a more primitive condition in the *Leanchoilia-Alalcomenaeus* clade and the convergent origin of a five-segmented head in Clade 3 (of Fig. 3.8) and the Xandarellida, are necessary to optimise this character (number 4, above) onto the most parsimonious cladogram. There are also transitions to autapomorphic states in *Emeraldella* and *Sidneyia*. In the case of *Sidneyia*, however, an argument could be made (following Bergström and Stürmer 1978, see discussion of Character 4, above) that the head consists of five segments, as in closely related taxa, but autapomorphically each segments has a separate tergite. This would further increase the phylogenetic stability of head segmentation. Also following Bergström and Stürmer (1978), the head of *Cheloniellon* could be considered to consist of two tergites, making it more similar to the head of *Emeraldella* (with six pairs of appendages).

The significance of the degree of fit of head segmentation to phylogeny was assessed using a randomization technique. This compared the pattern of head evolution described above with those expected if head segmentation was effectively random with respect to phylogeny. The length of Character 4 (when ordered) on the chosen tree was compared to the lengths obtained on the same tree when the observed character states were randomly reassigned to terminals. In each case, polytomies were resolved using parsimony. This procedure was automated in PAUP* following the technique described by Siddall (1998) for testing the significance of his Manhattan Stratigraphic Metric. The NEXUS format command files for these searches are shown in Appendix 6. Character 4 has a length of 16 on the chosen tree. Out of 20000 randomization replicates, in only seven was a length equal or lower than 16 found, giving a *P*-value of 0.00035 (see Figure 3.13A). In other words, assuming the phylogeny favoured above, the head tagma in arachnomorphs, far from evolving highly homoplastically, could hardly have evolved more parsimoniously. This result is unaffected by the use of head segmentation as a phlyogenetic character in determining the tree against which fit was tested. The strict consensus of 60 MPTs found with character 4 excluded (with some characters ordered and using the 'Aglaspidida2'

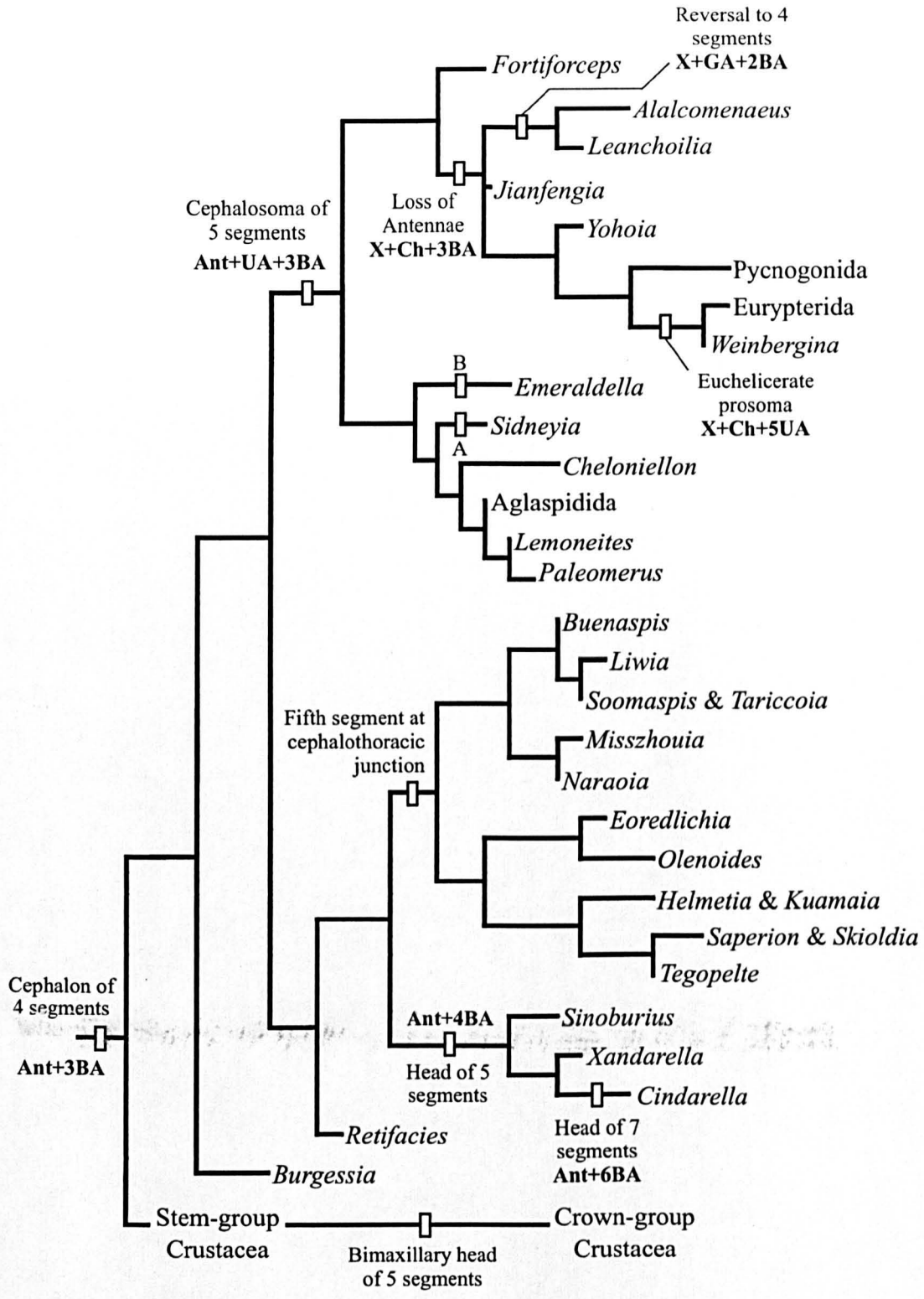


FIGURE 3.12. Cladogram from Figure 3.10 showing changes in head segmentation. Bold type shows abbreviated head segmentation formula: Ant, antennae; BA, biramous appendage pairs; Ch, chelicerae; GA, great appendages; UA, uniramous appendage pairs; X, segment without appendages. Synapomorphy A is the autapomorphic reduction in head length to a single segment in *Sidneyia*. Alternatively, may represent secondary division of the head shield. Synapomorphy B is the increase in the length of the head in *Emeraldella* to six segments.

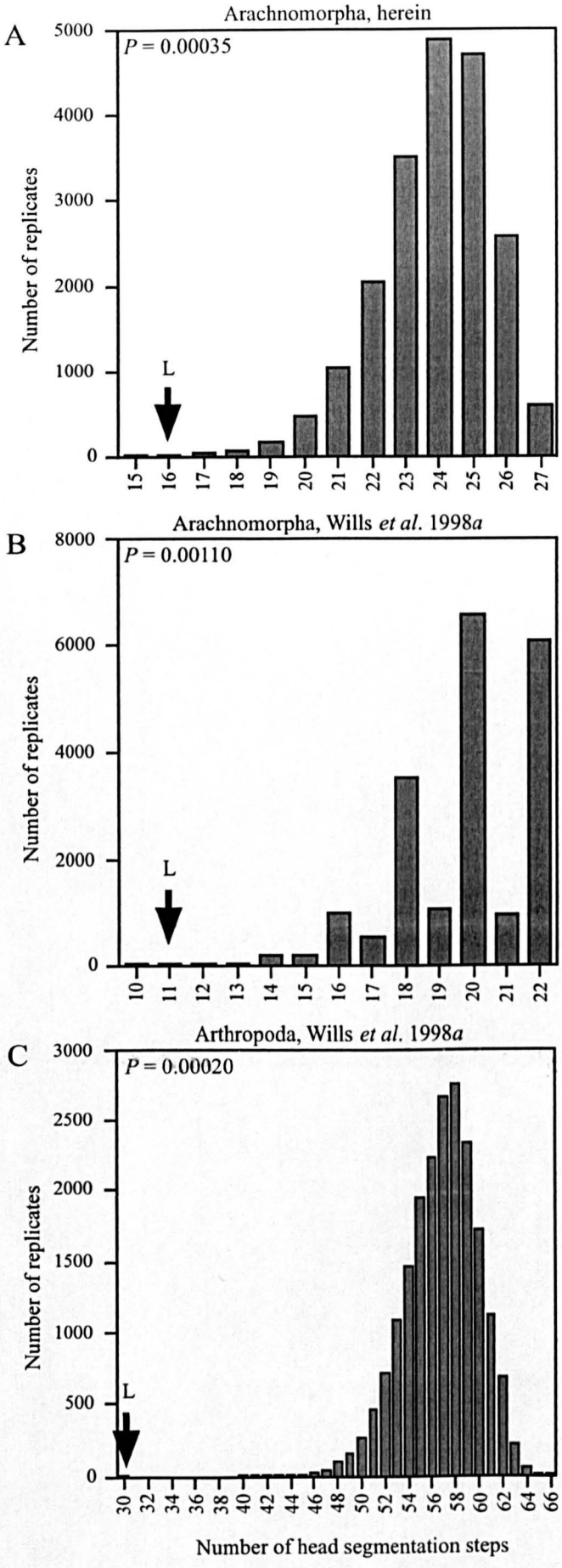


FIGURE 3.13. Results of 20000 replicate permutation tests of the significance of fit of head segmentation to phylogeny (see Appendix for PAUP* command files used to generate this data). 'L' indicates length of original, unpermuted data. A, Arachnomorpha, using data presented herein and the tree shown in Figure Y. B, Arachnomorpha, using data and majority-rule consensus tree presented by Wills *et al.* (1998*b*, table 2.1, figure 2.1). C, Arthropoda, other details as B.

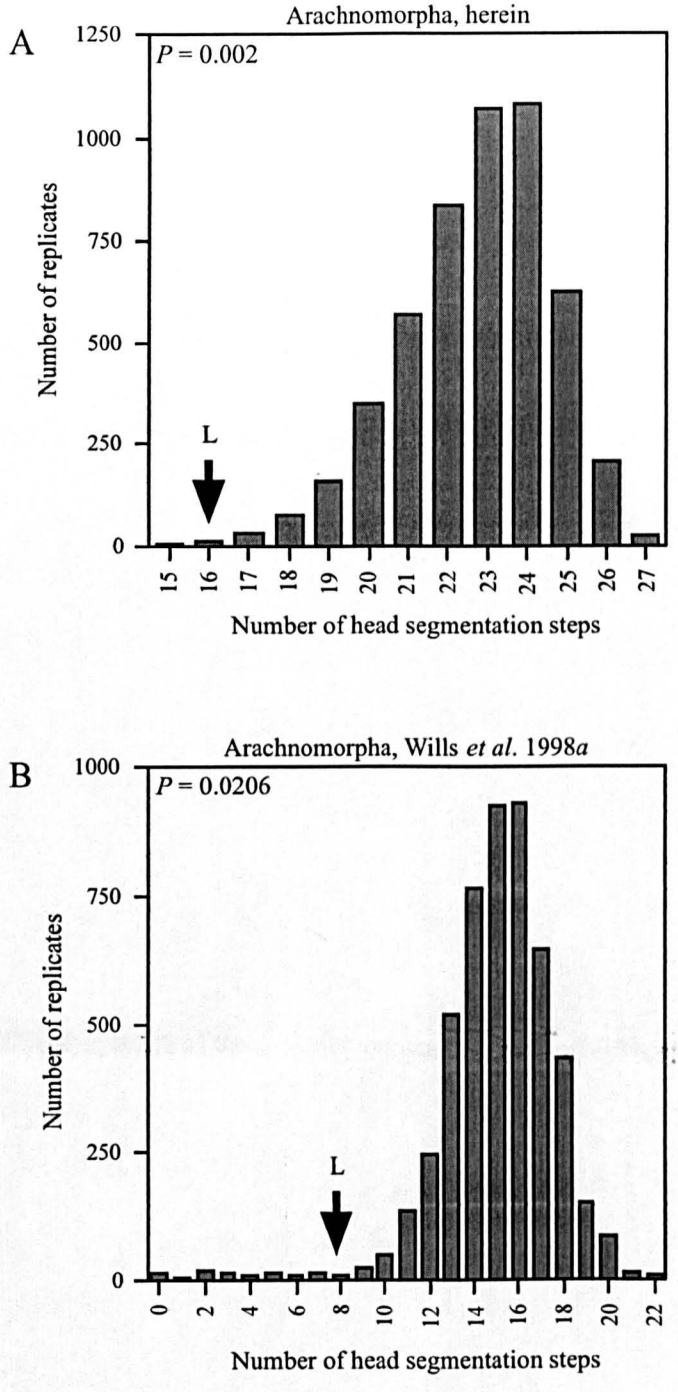


FIGURE 3.14. Results of 5000 replicate permutation tests of the significance of fit of head segmentation to phylogeny. 'L' indicates length of original, unpermuted data. A, Arachnomorpha, using data presented herein and the strict consensus tree from all analyses. B, Arachnomorpha, using data and strict consensus tree from Wills *et al.* (1998*b*, table 2.1).

coding) differs from the results with character 4 only by the degree of resolution. The same analysis was carried out on all arthropods and the arachnomorph clade on the basis of the majority rule consensus of Wills *et al.* (1998*a*) and their character 29. The data of Wills *et al.* (*op. cit.*) also indicate a significant fit. Using their data for all arthropods, the unpermuted data gave a much shorter length than any of the permutations ($P = 0.0002$, see Fig. 3.13C). In the case of arachnomorphs, 22 of the 20000 replicates showed a length equal to or less than that from the unpermuted data ($P = 0.0011$, see Fig. 3.13B). The fit for arachnomorphs was therefore less good with Wills *et al.*'s data than with the data presented here.

The use of less well resolved trees in these randomization tests provides a stricter test of the hypothesis. This is because during each replicate polytomies are resolved most-parsimoniously with respect to head segmentation and hence, with the same random assignment of character states, shorter trees may be found than with more fully resolved trees. Performing the test on less well resolved trees, however, is computationally more complex and many times slower. This is particularly the case when the number of segments is unknown in some taxa. Randomization tests were carried out with 5000 permutations for arachnomorphs on the basis of the analyses presented above and by Wills *et al.* (1998*a*), using the strict consensus tree shown in Figure 3.8 and that formed by collapsing nodes of the majority-rule consensus shown in figure 2.1 of Wills *et al.* (1998*a*). In both cases, the significance of the fit of head segmentation to arachnomorph phylogeny was confirmed (Fig. 3.14). The results again indicate that the hypothesis presented above suggests less homoplastic evolution of the arachnomorph head ($P = 0.002$) than that proposed by Wills *et al.* (1998*a*; $P = 0.0206$), but that in neither case are suggestions that head evolution was so convergent as to be taxonomic irrelevant supported.

4. AGNOSTID ORIGINS AND THE PHYLOGENY OF THE EODISCINIDS

AGNOSTIDS (Suborder Agnostina Salter, 1864) are a major component of Cambrian arthropod diversity. They are valuable biostratigraphic indices (e.g. Peng and Robison 2000), since they evolved rapidly and most genera and many species are cosmopolitan in their distribution (Robison 1984*a*). Agnostids originated early in the Cambrian (Rasetti and Theokritoff 1967; Blaker and Peel 1997) and survived until the late Ordovician (e.g. Shergold and Laurie 1997; Shergold, Laurie and Sun 1990). Agnostid morphology is remarkably conservative throughout this range, despite their high diversity (123 genera and subgenera according to Shergold and Laurie 1997, p. 332). For example, Öpik (1967, p. 65) argued that due to the 'combinative nature' of agnostid taxa 'all agnostoids within their suborder are relatively close to each other', a point of view that has been supported more recently by Shergold and Laurie (*op. cit.*), who suggested that 'Agnostina reiterate morphological conditions at different times in different family groups'. There has been a universal consensus that agnostids represent a highly distinctive and specialised body plan that differs morphologically from any other arthropod (see Fortey 1997, p. 294), e.g. 'It is not in question that Agnostina were highly specialized arthropods, with a whole series of autapomorphies' (Fortey and Theron 1994, p. 851). This specialised morphology has fuelled the profusion of discussions about agnostid life habits in the literature, which have spanned 'almost the whole range of possibilities open to marine arthropods' (Fortey 1985, p. 3).

The pattern of morphological evolution shown by agnostids - early origination of a distinct group that is subsequently morphologically conservative - is that regarded by Gould (1989) as typical of the Cambrian explosion as a whole. According to Gould's hypothesis (described in more detail in Part One, above) new higher taxa originated rapidly during the Cambrian explosion with highly distinct morphologies, resulting in a rapid increase in morphological disparity at low levels of diversity early in metazoan evolutionary history. During subsequent evolution taxonomic diversity increased with comparatively little increase in disparity. No other trilobite higher taxon

seems to illustrate Gould's hypothesis so clearly, and few are as widely accepted as monophyletic as the agnostids. The origin of the agnostids therefore represents an unrivalled opportunity to examine the origin of a major arthropod body-plan during the Cambrian.

A robust and detailed phylogenetic hypothesis of agnostid origins is a critical first step for any investigation of their origin and early evolution. Before such a hypothesis can be developed a monophyletic group including agnostids and their immediate relatives must be identified that is sufficiently small to be amenable to cladistic analysis, given constraints imposed by both the coding process and analytical complexity. In other words, the broad relationships of agnostids need to be clarified before the detailed pattern can be investigated. Testing the radically different hypotheses of agnostid relationships at the same time as analysing a taxonomic sample sufficiently dense to resolve detailed evolutionary patterns would necessitate construction of an impractically large cladistic matrix.

The agnostid problem

There has long been intense debate about the relationships of agnostids (see e.g. Fortey and Theron 1994; Fortey 1997; Shergold 1991). They are regarded conventionally as trilobites closely related to eodiscinids (Suborder Eodiscina Raymond, 1913). This hypothesis is reflected in the long history of uniting agnostids and eodiscinids to the exclusion of other trilobite groups (for which the term polymerid is used here) in Gürich's (1907) Isopygia, Jaekel's (1909) Miomera or most often recently, in the Order Agnostida Salter, 1864. However, some authorities have considered this to be a matter of convenience (since calcified agnostid exoskeletons are often preserved alongside those of polymerid trilobites) and not a reflection of relationships. Instead, many authors have suggested that agnostids are not trilobites at all but constitute a distantly related group with a

separate arthropod origin, usually considered to be close to crustaceans (Resser 1938; Walossek and Müller 1990; Shergold 1991).

Arguments against assigning agnostids to the Trilobita have relied on the supposed distinctiveness of agnostid morphology. Müller and Walossek (1987), for example, discussed the appendage morphology of the Upper Cambrian *Agnostus pisiformis*, which differs considerably from that of other trilobites (see e.g. Whittington 1997*b*) and Shergold (1991) has highlighted the lack of a protaspis larval stage in agnostids. Peng and Robison (2000, p. 11) identified four suites of characters which they considered unique to the Agnostina: the modification of the cephalo-thoracic articulation, the protuberant hypostome, the lack of segmentation of the pleural lobes of the pygidium and the presence of triangular basal lobes on the cephalic axis, and they excluded both condylopygoids and eodiscinids from the Agnostida. The development of cladistic reasoning, however, has made it clear that such unique features (autapomorphies) are of no consequence in determining relationships.

Of all the characters that have been discussed in the debate over agnostid relationships, the only potential synapomorphies uniting agnostids and non-trilobite arthropods are features of the appendages. Agnostid appendages are known only from exceptionally preserved specimens of *Agnostus pisiformis* from the Upper Cambrian Orsten deposits of Sweden (Müller and Walossek 1987). These appendages show a number of similarities, which have been considered derived, to those of supposed stem-group crustaceans from the same deposits (Walossek and Müller 1990, 1997; Bergström 1992; Hou and Bergström 1997). This evidence for crustacean affinities is ambiguous. Firstly, as discussed in Part 3 above, the primitive condition of the euarthropod exopod is unclear. Secondly, all of the Orsten material is of sub-adult individuals and the appendages of many arthropods, both fossil (including *Agnostus* and the supposed stem-group crustaceans) and living (e.g. Olesen and Walossek 2000, Schram and Koenemann 2001), show a remarkable degree of ontogenetic variation. All other described trilobite appendages are from adult specimens

(Whittington 1997*b*; Chatterton and Speyer 1997, p. 200) – it is possible that the appendages of immature polymerids resembled those of agnostids (e.g. Speyer and Chatterton 1989).

In contrast, a number of unambiguous synapomorphies uniting agnostids and other trilobites have been recognised, largely as a result of the work of Fortey (1990, 1997; Fortey and Theron 1994). These include the trilobation (particularly possession of a glabella) and calcification of the exoskeleton, the presence of a cephalic border, and the method of thoracic articulation. The inclusion of agnostids within a trilobite clade has been confirmed in wider analyses of arthropod phylogeny (e.g. Briggs *et al.* 1992*a*, 1993; Wills *et al.* 1994). In addition to synapomorphies uniting agnostids and trilobites as a whole, a much longer list of potential synapomorphies uniting agnostids and eodiscinids would need to be explained as a result of convergence if agnostids were excluded from the Trilobita (see e.g. Fortey and Theron 1994, text-fig. 8). In summary, the application of cladistic thinking has resulted in a compelling case for regarding agnostids as trilobites.

COMPARATIVE MORPHOLOGY OF AGNOSTIDS AND EODISCINIDS

The distinctive morphology of agnostids has resulted in the adoption of a specialised descriptive terminology for the group. The perception of morphological distinction, reinforced by terminological differences, has also resulted in a tendency for trilobite researchers to specialize in either agnostids or polymerids. This is illustrated by the separate description of agnostid and co-occuring polymerid and eodiscinid faunas by different authors – an approach very rarely applied to other trilobite groups. For example, the polymerid faunas of the Middle Cambrian Henson Gletscher and Cap Stanton formations of North Greenland were described by Babcock (1994) and the accompanying agnostids by Robison (1988,1994). Both the persistence of a distinct terminology and the paucity of researchers familiar with both agnostids and polymerids have in

turn led to a paucity of research on the comparative morphology of agnostids and other trilobites. Other factors, such as the largely geological as opposed to biological interests of the majority of Cambrian trilobite workers interested in agnostids, have also contributed to this. There is currently a considerable lack of clarity concerning the homology of many features of agnostids with those of other trilobites. For example, the axial segmentation of agnostids has been considered too distinctive to allow homologies with that of other trilobites to be drawn (e.g. Rushton 1966).

Here, the comparative morphology of agnostids and eodiscinids is thoroughly revised within the context of polymerid trilobite morphology. This discussion serves both to clarify the origin of agnostids, by identifying numerous synapomorphes uniting the Agnostina and eodiscinids, and to establish hypotheses of homology that form the basis of a large character distribution matrix. Cladistic analysis of this matrix results in a detailed hypothesis of the origin of agnostids.

Throughout this work informal names refer to taxa employed in the recent *Treatise on Invertebrate Paleontology*. Agnostid refers to the Agnostina, i.e. both Agnostoidea and Condylopygoidea, which are called agnostoids and condylopygoids, respectively. The term eodiscinid is used for the Eodiscina. No informal name is used for the Agnostida – the group including agnostoids, condylopygoids and eodiscinids.

Morphological comparisons

General similarities between agnostids and eodiscinids have long been recognised. For example, the two groups were united in Jaekel's (1909) Miomera or Kobayashi's (1939, 1944) Agnostida on the basis of a small number of thoracic segments, isopygy, and the loss of eyes and facial sutures. Since then a number of authors have identified other general similarities between agnostids and eodiscinids as a whole, including discussions of ontogeny by Rushton (1966, p. 10) and Jell (1970)

and similarities in the mechanism of enrollment discussed by Müller and Walossek (1987, p. 52). These similarities have been put into a cladistic context by Fortey (1990; Fortey and Theron 1994). However, in recent years, no general attempt has been made to systematically compare the morphology of the two groups.

Similarities between agnostids and particular eodiscinid taxa have been discussed less regularly, but the eodiscinid genera *Chelediscus* Rushton, 1966 and *Tannudiscus* Pokrovskaya, 1959 have been considered to share a number of features with agnostids (Rushton 1966; Jell 1975, 1997). Both these taxa are here included in the family Weymouthiidae (*cf* Jell 1997). *Chelediscus*differs from the other taxa included in the Calodiscidae by Jell (1997) in having a pointed glabella, a larger number of pygidial segments, genal spines and an occipital furrow that slope backwards dorsally in lateral view, among other characters. These features are all found in a number of weymouthiids.

Here, the homology of 11 character complexes in agnostids, eodiscids and polymerids is discussed and their probable phylogenetic significance established. In particular, the morphology of weymouthiid eodiscinids is compared to that of agnostids. The choice of characters for discussion is based primarily on previous discussions of agnostid morphology, although the significance of a number of characters is newly identified. All characters that have previously been claimed as agnostid synapomorphies are reassessed.

1. Blindness

All agnostids lack eyes and facial sutures, as do a number of eodiscinid taxa. It is widely accepted, following Jell (1975) and Öpik (1975), that blindness arose polyphyletically amongst eodiscinids. This may or may not be correlated with the loss of the facial sutures, since some eodiscinids possess eyes but lack facial sutures (e.g. *Yukonia intermedia* Palmer, 1968, pl. 2, fig. 14;

Helepagetia bitruncula Jell, 1975, pl. 29, fig. 9). A similar observation has been used (Fortey 1990, p. 563) to suggest different modes of eye loss in various clades formerly included in the polyphyletic ptychopariid family Conocoryphidae (see Cotton 2001). Jell (1975, 1997) recognised at least three independent origins of blindness within the eodiscinids, within his families Calodiscidae and Eodiscidae and in the origin of the family Weymouthiidae. Other lineages may also have lost their sight convergently (e.g. Jell *in* Bengtson *et al.* 1990, p. 258). Blindness may have evolved independently a fourth time in the origin of the Agnostina from eodiscinid ancestors but, unless other evidence suggests otherwise, it is most parsimonious to assume that the agnostids evolved from a blind, sutureless eodiscinid.

2. Cephalic outline

Kobayashi (1943, p. 45; 1944, p. 10) differentiated the agnostids and eodiscinids partly on the basis of the difference in cephalic outline. However, as Fortey and Theron (1994) recognised, certain eodiscinids have a cephalic outline more similar to agnostids than to either other eodiscinids or typical polymeroid trilobites. In most eodiscinids and polymeroids, the cephalon is considerably wider (transversely) than long (sagittally) and is widest at the posterior margin. In agnostids and a number of weymouthiid taxa including *Chelediscus acifer* Rushton, 1966, *Jinghediscus numularius* Xiang and Zhang, 1985, and *Tannudiscus balanus* Rushton, 1966, the cephalon is as long or longer than it is wide, and is widest at a point well anterior of the posterior margin. If the Agnostida are regarded as having polymerid ancestors, the situation in these eodiscinids and agnostids is derived. This is also supported by the distribution of cephalic outline amongst eodiscinids. In the earliest occurring species and those that have been considered primitive, such as *Tsunyidiscus*, *Sinodiscus* and *Calodiscus*, the cephalon is particularly wide compared to its length. In other eodiscinids this ratio is higher. This change in the shape of the

cephalon therefore appears to represent a valid synapomorphy uniting at least some of Jell's Weymouthiidae with the Agnostina.

Examination of the ontogeny of polymeroid trilobites suggests that this character may reflect the probable progenetic origin of agnostids, since the cephalic outline is highly variable in the early ontogeny of many basal trilobites. The meraspid cephalon of most polymeroids has an outline more similar to agnostids than that of the typical holaspid cephalon. This seems to be particularly true of primitive polymeroids, as illustrated by Chatterton and Speyer (1997, figs 168-169) and Zhang and Pratt (1999).

Isopygy has long been recognised as a distinctive feature of agnostids and has most recently been discussed by Fortey (1990; Fortey and Theron 1994). The similarity in outline between the cephalon and pygidium is, however, also a feature of all eodiscinids where the pygidium is known, and represents a potential synapomorphy at the level of Agnostida.

3. Genal spines

Fortey (1990, text-fig. 14) used the character 'genal spines reduced or absent' as a synapomorphy uniting agnostids and eodiscinids to the exclusion of other trilobites but provided no discussion of this character. The best known eodiscinid taxa (i.e. Eodiscidae, see e.g. Jell 1975, pls 17-19) and many agnostids do indeed lack, or have much reduced, genal spines.

Öpik (1979) suggested that agnostids lack genal spines and that the spines near the genal angles of agnostids instead represent 'fulcral spines' or 'fulcral prongs'. Müller and Walossek (1987) also employed this terminology. However, neither Öpik nor Müller and Walossek present a detailed argument in support of this view. It is true that the short agnostid spines are directly dorsal to the sockets against which the first thoracic segment articulates, whereas in most trilobites a distinct fulcral point lies abaxial to the genal spines on each side of the cephalon. In adult

agnostids the posterior cephalic spines are positioned considerably dorsal to the lateral cephalic margin in lateral view. In the majority of trilobites, the genal spines lie on the same plane dorsoventrally as the lateral cephalic margin. The short, triangular agnostid 'prongs' are also structurally distinct from the typically long and slender genal spines of other trilobite groups. These observations could be interpreted as supporting the non-homology of agnostid posterior cephalic spines with the genal spines of polymeroids.

However, during the ontogeny of *Agnostus pisiformis*, the 'fulcral prongs' can be seen to migrate medially and dorsally with respect to the lateral cephalic margin (Müller and Walossek 1987, figs 10, 12). In the youngest growth stages observed they are at the ventral extreme of the cephalon in lateral view and close to the lateral extreme in dorsal view – essentially the same position as conventional polymeroid genal spines. The strong geniculation between the lateral margin and the genal spines develops gradually through ontogeny. Similarly, the spines are relatively much longer in early growth stages than in later ones.

Within the eodiscinids, taxa with genal spines similar to those of polymeroids and taxa with agnostid 'fulcral spines' are known. This was recognised by Öpik (1973, table 6), who considered that *Eodiscus* possessed genal spines, but *Pagetia* fulcral spines. These taxa are generally considered to be very closely related. Within the Weymouthiidae, *Litometopus longispinus* has long genal spines that are distinctly abaxial to the fulcral points (Rasetti 1967, pl. 3, fig. 3; pl. 8, figs 1, 4), whereas *Bathydiscus dolichometopus* has very short spines directly dorsal to the fulcra and well inside the lateral margins of the cephalon (Rasetti 1967, pl. 1, fig. 3; pl. 9, figs 1, 4).

A number of eodiscinids, in particular weymouthiids, and agnostids have long genal spines of typical trilobite type. Genal spines are universally present in condylopygoids, which are generally considered to be the sister-group of agnostoids. It may be that genal spines are convergently reduced in agnostoids and eodiscinids, and that both primitive agnostids and primitive eodiscinids possessed genal spines comparable to those of polymeroids. When the

phylogeny of the eodiscinids is better known, the significance of the variation in genal spine morphology may become clear. However, spines of very similar morphology to the posterolateral cephalic spines of agnostids are found in eodiscinids, and there seems to be no reason to regard agnostid spines as fundamentally different from those of polymeroids.

4. Glabellar segmentation

A distinct terminology has been applied to the glabellar segmentation of agnostoids, following Robison (e.g. 1964, 1982). The glabella is divided by a complete transglabellar furrow into an anteroglabella and posteroglabella. The posterior portion of the posteroglabella projects posteriorly, between more or less triangular basal lobes, as the glabella culmination (*sensu* Whittington 1997*a*). This may be rounded or angular and bears a distinct small node in many taxa. These basal lobes and the narrow (sag. and trans.) occipital band which runs between them demarcated by shallow basal furrows, are excluded from the glabella. The lateral furrows of the glabella are numbered F1 to F3 from the posterior forward, F3 being the transglabellar furrow, and the axial rings defined by these furrows at the anterior margin are numbered M1 to M3 respectively. This terminology has not been applied to the Eodiscina. Jell (1975), for example, regarded the basal lobe of the eodiscinid cephalic axis as occipital, and used the notation S and L for glabellar furrows and lobes, as applied to other trilobites.

Despite the use of a distinct terminology, it seems that most authors have considered the agnostid cephalic axis to be directly homologous with the polymeroid glabella, the basal lobes and occipital band making up a modified occipital ring and the transglabellar furrow a modified pair of lateral glabellar furrows. Fortey (1994, table 1), Hunt (1967), Robison (1984*a*, p. 9) and Whittington (1965), for example, all regarded the basal lobes as occipital. Whilst other authors (Peng and Robison 2000, p.11; Müller and Walossek 1987, p. 51) expressed doubt that the basal

lobes represent the occipital ring, no coherent alternative has been proposed. The suggestion that the occipital band and basal lobes make up the segmental homologue of the axial rings of the thorax (Öpik 1979, p. 30; Müller and Walossek 1987, p. 51) can be applied equally to the polymeroid occipital ring.

Most trilobites possess four pairs of lateral furrows anterior to the occipital furrow. It is therefore unclear to which polymeroid furrows the three pairs in agnostids are homologous. In particular, the transglabellar furrow may represent S3 or S4 and the homologues of the polymeroid S1, S2 or S4 furrows may be missing in agnostids. If either the S1 or S2 furrows are missing then the posteroglabella represents L1 through L4 and the anteroglabella L5. If, on the other hand, the S4 furrows are missing then the anteroglabella would represent both the L4 and L5 lobes. The latter scenario seems more likely given that the S4 furrows are weak or effaced in many polymeroid trilobites.

Agnostid specimens showing presumed muscle attachment sites on the ventral surface of the exoskeleton support the homology of the agnostid transglabellar furrow with the polymeroid S3 furrows. Specimens of *Galbagnostus galba* (Whittington 1965, pl. 3, fig. 7, 15; pl. 3, fig. 9), clearly show four pairs of smooth areas anterior to the basal lobes. Judging from their distribution along the glabella, two of these pairs are on the anteroglabella and two on the posteroglabella. This suggests that the two main divisions of the agnostid cephalic axis each consist of two segments.

The insertion of the genal caecae, in taxa where these are well developed, also suggest that it is the homologue of S4 that is missing in agnostids. In polymeroids a similar caecal network underlies the dorsal exoskeleton of the genae and inserts into the glabella at the same point as the eye ridges (e.g. *Meneviella venulosa*, Cotton 2001, Text-fig. 1a). This branch of the caecal network is commonly overlain by the eye ridges but is clearly visible, for example, in blind polymeroid taxa (Cotton 2001, p. 173-174). In all polymeroids the eye ridges (and hence the caecal network) insert into the glabella anterior to the S3 furrows but posterior to the S4 furrows. In many agnostids, where the caecae are well developed, they seem to insert just anterior to the

transglabellar furrow. This is indicated by a shallowing of the axial furrows at the point of insertion – just as the insertion of the caecal network in blind polymeroids is indicated by a shallowing of the axial furrows (Cotton 2001, p. 188; see *Pseudatops reticulatus*, pl. 2, fig. 1; *Alacephalus contortus*, pl. 1, fig. 6). This assumes that the agnostid caecae are homologous with those of polymeroids.

The transglabellar S3 furrow is also a general feature of eodiscinids. Taxa with transglabellar furrows are known from all eodiscinid families and in most species lacking the transglabellar furrow all lateral furrows are effaced. Few species (such as *Discomesites fragum* Öpik 1975, pl. 5, figs 1-4) possess strong, divided S3 furrows. The transglabellar S3 furrow is likely to be a distinctive synapomorphy uniting agnostids and all eodiscinids. Even in eodiscinids where the frontal lobe is very long and the lateral furrows well impressed (such as *Serrodiscus daedalus*, Blaker and Peel 1997, fig. 25.3,9-11), no furrows are present anterior to the transglabellar furrow. Complete effacement of the S4 furrow therefore also characterises eodiscinids and agnostids although, as mentioned above, this character has a wide distribution amongst trilobites.

5. Form of the occipital ring

The structure of the cephalic axis in eodiscinids is highly variable. In some taxa, such as *Sinodiscus* (Zhang *et al.* 1980, pl. 4, figs 12, 18-19, 21) and *Korobovia ocellata* (Jell *in* Bengtson *et al.* 1997, figs 177A-F), it differs from the primitive polymeroid condition only by the loss of the S4 furrows and presence of a transglabellar S3. In such cases, the occipital furrow is approximately straight or slightly curved posteriorly across the axis (in dorsal view). In lateral view the furrow is directed dorsally approximately perpendicular to the plane of the cephalic margin. The occipital ring is either of uniform width or slightly wider (sagitally) dorsally than ventrally with the result that, in lateral view, the posterior margin of the ring is angled backwards.

The occipital ring is highly modified in most eodiscinids. The occipital ring is more or less strongly angled backwards, with the result that the occipital furrow is angled backwards dorsally in lateral view and the occipital ring is lower (dorsoventrally) than the posterior lobe of the glabella. In some taxa (e.g. *Bathydiscus dolichometopus* Rasetti 1966, pl. 9, fig. 3) this feature is present without any modification of the glabella anterior of the occipital furrow. Usually, however, the medial part of the occipital ring is completely covered dorsally by a posterior projection of the glabella. In these cases the occipital ring, in dorsal view, consists of two sub-triangular lateral lobes connected by a (sag.) narrow band behind or underneath the glabellar projection. This situation is strongly reminiscent of the agnostid basal lobes and occipital band, and I can see no reason not to regard these modifications of the occipital ring and posterior glabella as homologous.

The form of the glabellar projection differs between eodiscinid groups. In weymouthiids it is posteriorly rounded, as in the majority of agnostids, but in most members of the eodiscinid families Yukoniidae and Eodiscidae the glabella is extended into a long posterodorsally directed spine. In these groups, the occipital ring is divided and, in some cases, faint furrows continuing the line of the deep lateral furrows run up the length of the spine (Rushton *pers. comm.*). This 'cranidial spine' therefore consists of a glabellar expansion and part of the occipital ring (Jell 1975, p. 4) and is not closely comparable to the situation in weymouthiids and agnostids. The backward expansion of the glabella may therefore not be homologous between agnostids and all eodiscinids, but the rounded expansion over a complete occipital furrow in agnostids and weymouthiids seems a convincing synapomorphy. Division of the occipital ring into an occipital band and basal lobes by the band furrow (*sensu* Whittington and Kelly 1997, p. 315) in agnostids is also shared by the two species of the eodiscinid genus *Chelediscus* (Rushton 1966, p. 20).

The backward displacement of the occipital ring is likely to have had a function during enrollment. It is likely that, when fully extended, the thorax of many eodiscinids would have been angled ventrally with respect to the plane of the cephalic border due to the angle of the occipital ring, as discussed for *Agnostus pisiformis* by Müller and Walossek (1987). This decreases the

degree of flexion necessary between the cephalon and the thoracic segments during complete enrollment of the short thorax.

Finally, the presence of a spine on the occipital band has been recognised as a distinctive feature of condylopygoids (Rushton, 1966, p. 29). Some weymouthiid eodiscinids also have an occipital spine (e.g. *Leptochilodiscus punctulatus* Rasetti 1967, pl. 3, figs 18-20) but is unknown in any agnostoid. This character may therefore not represent a valid synapomorphy of the Condylopygoidea, since it may be inherited from an eodiscinid ancestor. In this case, the loss of the occipital spine may instead be a synapomorphy of the Agnostoidea. The phylogenetic significance of this character will only be resolved when the sister-taxon to the agnostids within the Weymouthiidae is more precisely identified.

6. Median glabellar node

The median glabellar node on the dorsal midline of the posteroglabella has generally been considered a distinctive agnostid character. The position of this node is somewhat variable. In some taxa (e.g. *Goniagnostus fumicola*, Öpik 1961a, pl. 20, figs 14-17, *Ptychagnostus atavus* Peng and Robison 2000, fig. 52.1-3). it is at the level of the S1 furrows, in others (e.g. *Oidalagnostus trispinifer*, Peng and Robison 2000, fig. 42.10-11) it is at the level of the S2 furrows. It seems clear, however, that the node belongs to the L2 glabellar lobe. The variation in the position of the node compared to the lateral furrows in dorsal view could easily be explained by changes in the dorsoventral orientation of L2.

Accepting the furrow homology scheme discussed above, in a number of weymouthiid taxa L2 bears a dorsally directed spine that is likely to be homologous to the median glabellar node of agnostids. In some cases the glabella is so strongly expanded posterodorsally (e.g. *Acimetopus bilobatus* Rasetti 1966, pl. 4, figs 3-4) and/or the lateral furrows are effaced (e.g. *Serrodiscus*

ctenoa, see Rushton 1966, p. 15), so that the position of the spine in terms of glabellar lobes is impossible to determine. In such cases, however, it seems most likely that the spine is homologous with those that are clearly on L2 in other species such as *Acidiscus theristes* (see Rushton, 1966, text-fig. 4) and *Bolboparia canadensis* (Rasetti 1966, pl. 5, fig. 13). In some other weymouthiids only a low node is preserved, and it is unclear whether or not this was the base of a spine originally (e.g. *Tannudiscus balanus*, Rushton 1966, pl. 3, figs 9a, 10).

7. Sagittal pre-glabellar furrow

Very few polymeroid trilobites have a furrow running from the anterior of the glabella to the anterior cephalic border furrow. The sagittal pre-glabellar furrow, however, has rather a wide distribution within the eodiscinids and agnostids. It seems likely to have been acquired (or lost) convergently in many lineages in both groups. In the Eodiscina, *Natalina* (see e.g. *Natalina incita*, Repina and Romanenko 1978, pl. 6, fig. 15) in the Hebediscidae, *Chelediscus* (e.g. *Chelediscus chathamensis* Rasetti 1967, pl. 3, figs 14-15) in the Weymouthiidae and all genera of the Eodiscidae (e.g. *Pagetia fluvata* Jell 1975, pl. 8, figs 9, 12; *Helgeocia truncula* Jell 1975, pl. 29, figs 1, 5-6) have such a furrow. Similarly, the pre-glabellar furrow may be present or absent in agnostoid taxa thought to be closely related. For example, within the Ammagnostidae (sensu Peng and Robison 2000) the genus *Nahannagnostus* (e.g. *N. nganasanicus* Rozova 1964, see Peng and Robison, fig. 16) has a long, well-developed pre-glabellar furrow but *Kormagnostus* (e.g. *K. minutus*, Peng and Robison, fig. 24) lacks the furrow altogether. Given this distribution, the phylogenetic importance of this character is unclear. It seems likely that this distribution is a function of the expression or effacement of the furrow rather than the presence or absence of a significant underlying structure.

8. Hypostoma

The hypostome of *Agnostus pisiformis* described by Müller and Walossek (1987) is strikingly different from that of any known polymeroid. This has led to some authors rejecting the homology of agnostid and polymeroid hypostomes (Ramsköld and Edgecombe 1991). However, a range of hypostomal morphology is known from the agnostids. The hypostome of *Oidalagnostus trispinifer* (Robison 1988, fig. 9) is very similar to those of many polymeroid hypostomes and that of *Peronopsis interstricta* (Robison 1972, figs 1c, d, 4a-c) is somewhat intermediate between that of *O. trispinifer* and the *Agnostus* hypostome (Müller and Walossek, 1987, fig. 26). Few eodiscinid hypostomes have been identified, and nothing is known of the ventral morphology of weymouthiids. The hypostome of *Pagetia ocellata* (Jell 1975, pl. 28, figs 1-2) closely resembles that of ptychopariid polymeroids (Fortey 1990). Agnostid hypostome morphology provides no support for a non-trilobite origin of the group and in most taxa is not fundamentally different from that of polymeroids. Clearly, considerable evolution of the hypostome occurred within the agnostoids.

9. Thoracic segments

The presence of only two or three segments in the thorax of agnostid and eodiscinids was historically the basis for the division of the Trilobita into the subclasses Miomera and Polymera. More recently, this criterion has been rejected by some authors following the discovery of other taxa with few thoracic segments in the Corynexochida (*Thoracocare*, see Robison and Campbell 1974) and Raphiophoridae (Zhang 1980). Such discoveries, however, have no bearing on the status of this character as a potential synapomorphy for the Agnostida, albeit not a unique one. Further

reduction of the number of segments from three to two is likely to be a synapomorphy for a narrower clade including agnostids and some eodiscinids. However, like the loss of eyes and sutures, this is likely to have occurred polyphyletically - many of Jell's eodiscinid families include taxa with two segments and those with three segments. Within the Weymouthiidae, only *Chelediscus acifer* Rushton, 1966 is known to have possessed a holaspid thorax of only two segments, but the thorax is unknown in the majority of taxa.

Beyond this simple character the agnostid thorax is highly distinctive. Compared to most trilobites the axis is wide relative to the width of the segment as a whole and is divided into a median lobe and two lateral lobes by a pair of furrows. These characters are seemingly unique to agnostids. Additionally, the first thoracic segment is narrow (trans.) compared to the second, and the pleural tips of the first segment are angled backward whilst those of the second segment are angled forwards. These characters are clearly of importance during enrollment and are shared with at least some eodiscinids, such as *Chelediscus acifer* (Rushton, 1966, text-fig. 6). The angle of the pleural tips is shared more widely, including e.g. *Costadiscus minutus* (Eodiscidae; Babcock 1994, fig. 29.3-4) and *Tsunyidiscus niutitangensis* (Zhang *et al.* 1980, pl. 5, fig. 3). These taxa have thoracic segments of approximately equal width (trans.), but the pleural tips of the third segment are pointed forwards.

Öpik's (1979) suggestion that the widening and division of the occipital ring into basal lobes and the similar modification of the thorax in agnostids are linked evolutionarily is not supported by examination of weymouthiids. The division of the occipital ring in *Chelediscus* is not accompanied by division of the thoracic axial lobes.

10. Cephalothoracic articulation

The agnostids share a special type of articulation between the cephalon and the thorax that is unknown in other trilobites. The anterior thoracic segment of agnostoids and condylopygoids lacks

an articulating half ring with the result that, on enrolment, a small gap, the 'cephalothoracic aperture', is left between the axial lobe of the thorax and the occipital band of the cephalic axis (which, as argued above, represents the median part of the occipital ring). This was first recognised in agnostoids by Robison (1964, p. 515; 1984*a*, fig. 31) and in condylopygoids by Rushton (1979, p. 45). No similar structure has been described from any eodiscinid, although the thorax is unknown in a majority of species.

11. Segmentation of the pygidial axis

The form of the agnostid pygidial axis has probably been more widely regarded as highly distinctive than any other feature of the agnostids. Rasetti (1948) suggested that '... the agnostid pygidium is a very different structure from the usual pygidium of the other trilobites, including the eodiscids.' Many authors have considered the agnostid pattern of axial segmentation impossible to homologise with that of other trilobites. This has led those authors who accepted a relationship between agnostids and eodiscinids to propose that the agnostid segmentation was secondarily derived from a primitively unfurrowed axis (Henningsmoen 1951, p. 181; Palmer 1955; Rushton 1966, p. 10). Rushton further suggested that this was retained in Early Cambrian taxa such as *Condylopyge amitina* Rushton (1966, p. 29, pl. 4, figs 1-12) and *Peronopsis roddyi* (Resser and Howell 1938; see Blaker and Peel 1997, p. 26, figs 13-16, 25.4-5, 7).

The agnostid pygidium is characterised by a usually well-defined axis that is variable in both outline and length and which only bears furrows anteriorly. The pygidial margin of most condylopygoids and many agnostoids is equipped with one pair (or occasionally more) of broad based, flattened marginal spines extending posteriorly in the plane of the border. In condylopygoids three pairs of pygidial ring furrows are defined, whereas in most agnostoids only two pairs of furrows are present. It is widely accepted (following Palmer 1955; Öpik 1963, 1967)

that the agnostid posteroaxis consists of a number of segments which are not defined on the dorsal surface. These segments are sometimes indicated by small rounded pits or muscle insertion scars (termed notulae), and vary from four to nine in number (Öpik 1967, p. 67). In agnostoids a prominent node (hereafter, the axial node) is present on the second axial ring and a small node or nodes (posterior nodes) on the undivided posteroaxis. Robison (1984*a*, p. 17, 1988, p. 42; Peng and Robison 2000, p. 11) has repeatedly argued against interpreting these nodes of agnostoids as phylogenetically significant. I agree that the presence of the terminal and other posterior nodes may be a somewhat unreliable character, since these nodes are generally very weak and their presence may be polymorphic within species. However, those that can be associated unambiguously with the terminus of the intranotular axis should be considered homologous (Pratt 1992, p. 31). Secondly, in a majority of taxa showing multiple posterior nodes (reviewed by Peng and Robison 2000, p. 11), one of these nodes is associated with a transverse sulcus (in the terminology of Robison 1988, p.32; the 'rosette' of Öpik 1979, p. 19) which is likely to be phylogenetically significant and should not be dismissed as 'iteratively evolved' (Peng and Robison 2000, p. 10) without good evidence. The presence of the prominent axial node on the second segment, however, is constant in the group. In a number of taxa this is produced into a long spine (reviewed by Öpik 1979, table 5). In condylopygoids spines or nodes may be present on all three of the anterior axial segments, but that on the second segment is generally the most prominent (e.g. *Pleuroctenium granulatum*, see Rushton 1979) and can be regarded as homologous with the anterior axial node of the agnostoid pygidium.

The eodiscinid axis, in contrast, is generally fully segmented, although the ring furrows are effaced in a number of taxa. The number of segments in the eodiscinid pygidium is highly variable, particularly in weymouthiids, where it ranges from 6 (e.g. *Chelediscus acifer* Rushton 1966) to at least 11 (*Bolboparia elongata* Rasetti 1966, p. 20, pl. 5, figs 12-13), a similar range to that found in agnostids. Two patterns of axial nodes and spines can be distinguished amongst eodiscinids. Firstly many taxa show segmental spines which, when not present on all axial rings,

are generally effaced posteriorly (e.g. *Acidiscus birdi*). Secondly, many eodiscinids have a long, broad-based spine on a single axial segment (sometimes along with segmental nodes or spines on other segments). The best known of these are the terminal or sub-terminal spines of many Eodiscidae (e.g. Jell 1975). In weymouthiids such spines are generally on the anterior part of the axis and often on the second segment (e.g. *Acimetopus bilobatus* Rasetti 1966; *Bolboparia elongata* Rasetti 1966). As well as being on the homologous segment these spines resemble the anterior axial node of agnostids in distorting the ring furrows, which medially bend anteriorly and posteriorly to accommodate the broad base of the spine. This is very similar to the situation described, for example, by Ruston (1966, p. 29) for ptychagnostids. Possession of a prominent node or spine on the second pygidial segment may therefore be a good synapomorphy uniting agnostids and some weymouthiids. The homology of these spines across all Agnostida, however, is problematic because their position seems to be extremely plastic (see for example, Blaker and Peel 1997).

The effacement of the posterior axial furrows remains a good synapomorphy for the Agnostida. In eodiscinids with effaced ring furrows, all the furrows are more-or-less evenly effaced. In trilobites, furrows on the dorsal surface form ridges projecting ventrally which are generally considered to provide attachment sites for muscles acting on the appendages (e.g. Fortey and Owens 1999*b*). The loss of the posterior pygidial furrows in agnostids may therefore be explained by Müller and Walossek's (1987) observation that there were only three pairs of appendages under the pygidium of *Agnostus pisiformis*. This is supported by the presence of three pairs of notulae on the anteroaxis of the agnostid pygidium (see e.g. *Rhaptagnostus cyclopygeformis* [Sun, 1924], as illustrated by Shergold *et al.* 1990, fig. 16.3b; Shergold and Laurie 1997, fig. 233.3a; *Lejopyge calva* Robison 1964, illustrated by Robison 1984*a*, fig. 24). Reduction of segmentation of the pygidial axis in Agnostida is likely to have been associated with reduction and loss of the posterior pygidial appendages.

No obvious homologues of the paired marginal spines can been identified amongst the eodiscinids, despite the considerable range of spinose margins known in the group (see e.g. Rasetti 1966; Jell 1997). Pygidial spines in the Agnostida as a whole are probably modified from the segmental, laterally directed, marginal spines of polymeroid pygidia. The paired marginal spines have such a wide distribution (including all condylopygoids) that they are likely to be an agnostid synapomorphy, and their loss in some agnostoids a reversal.

The final feature of the agnostid pygidium that requires comment is the absence of pleural furrows, which is shared with all weymouthiids except *Stigmadiscus stenometopus* (Rasseti 1967, pl. 5, figs 1-4) and a few other eodiscinid taxa. Since the presence of pygidial pleural furrows is a feature of most eodiscinid and polymeroid trilobites it seems likely that it is plesiomorphic for eodiscinids. The loss of pleural furrows is therefore probably a synapomorphy of a weymouthiid-agnostid clade.

Discussion

The considerable number of detailed similarities identified above between agnostids and some eodiscinids represents a convincing argument that the distinctiveness of the Agnostida has been considerably overstated, and strongly supports previous arguments that the agnostids are trilobites. In a cladistic context, a number of the characters previously thought to be synapomorphies of the Agnostida are instead likely to be synapomorphies of various nested clades uniting agnostids with some eodiscinids. The likely distribution of the characters discussed above within the Agnostida (Figure 4.1) provides evidence that the Eodiscina is paraphyletic with respect to the Agnostina, as Jell (1975, 1997) and Zhang (*in* Zhang *et al.* 1980) suggested. The 'derived weymouthiid' group that is particularly close to the agnostids is unlikely to be monophyletic. Instead, some weymouthiids are likely to be more closely related to agnostids than others.

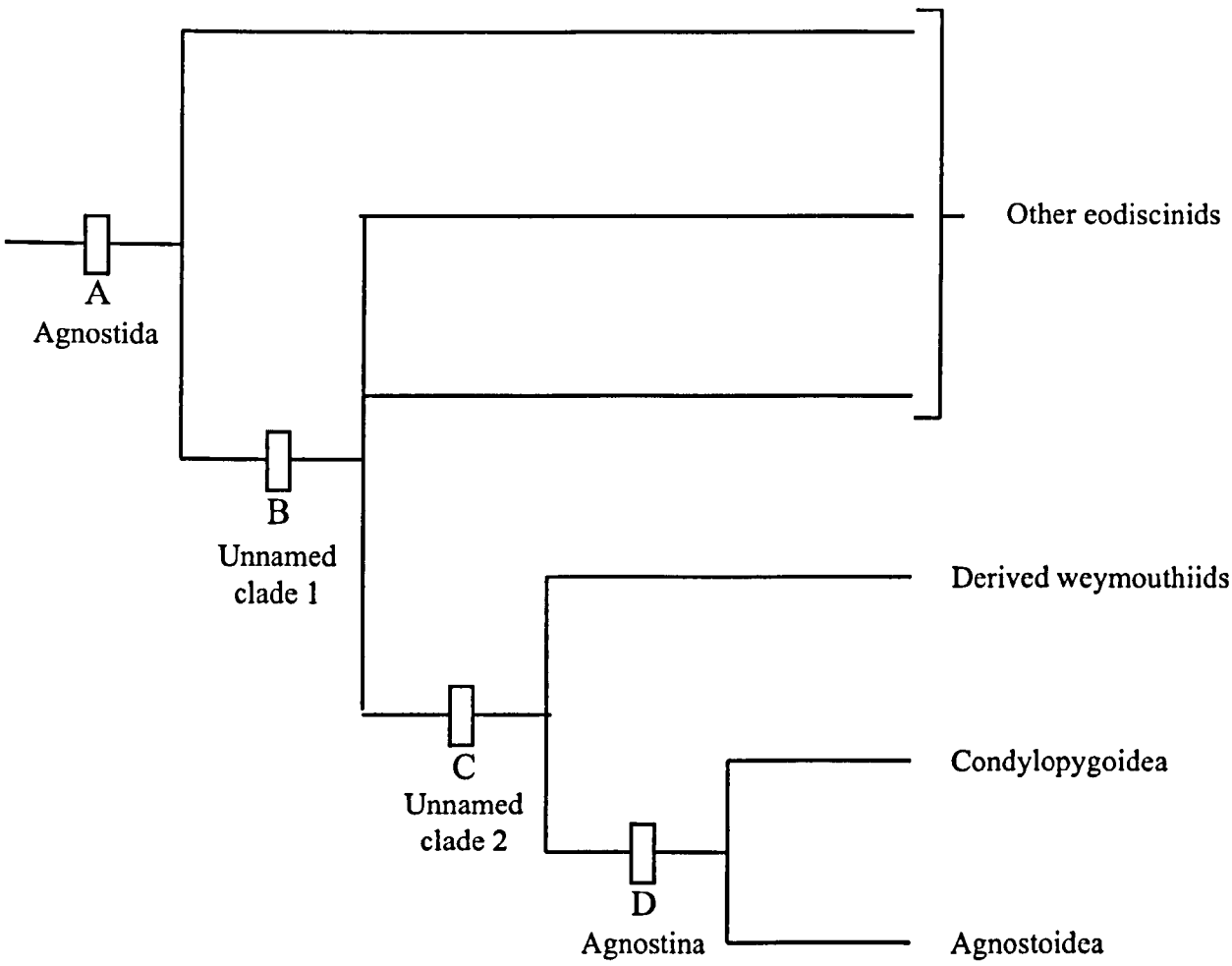


FIGURE 4.1. Cladogram illustrating the probable status of characters discussed in the text under Comparative Morphology. Synapomorphies for lettered clades: A. Agnostida - thorax of two or three segments, isopygy, transglabellar S3 lateral furrows, effacement of S4 furrows (4 synapomorphies). B. Unnamed clade 1 - blindness, loss of facial sutures, LO angled posteriorly, loss of pygidial pleural furrows (4 synapomorphies). C. Unnamed clade 2 - spine or node on L2, broad based spine on second pygidial segment, two thoracic segments, first thoracic segment transversely narrow compared to second, glabella expanded posterodorsally over LO, LO divided into median and basal lobes, rounded cephalic outline. (7 synapomorphies). D. Agnostina - loss of segmentation of posterior axis of the pygidium, division of thoracic axial rings into median and lateral lobes, cephalothoracic aperture (loss of articulating half-ring of the first thoracic segment), paired spines on posterior margin of pygidium (4 synapomorphies). Characters of uncertain significance - sagittal preglabellar furrow, occipital spine, thoracic axial spines or nodes, loss of rostral plate, loss of protaspis, modification of appendages, modification of hypostome, reduction of genal spines. Plesiomorphies - vertical undivided LO, long genal spines, furrowed pygidial pleurae, proparian sutures.

A range of authors have explicitly supported the view that there are no intermediate forms between agnostids and other trilobites (e.g. Kobayashi 1939, p. 73; Fortey 1997, p. 295). The analysis presented above suggests that the widely held view that 'a suite of species connecting [agnostids] with some other taxon is not known' (Fortey 1997, p. 295) is incorrect and that the Weymouthiidae constitute just such a suite. Of the characters discussed above, more support a clade of weymouthiids and agnostids than support the monophyly of the agnostids.

Confirming that agnostids are trilobites close to eodiscinids allows further analysis of the origin of the agnostids by limiting the scope of taxa that need to be considered, making the problem amenable to cladistic analysis. Since eodiscinids are in all probability paraphyletic with respect to agnostids, only eodiscinids need to be considered in a detailed phylogenetic analysis of agnostid origins.

PHYLOGENY OF THE EODISCINA

The classification of eodiscinids has been remarkably unstable, even compared to that of other Cambrian trilobite groups, and the few attempts to resolve the phylogeny of the group have been largely unsuccessful. The phylogeny of the Eodiscina is therefore of considerable interest in itself, as well as because of its significance for the understanding of the origins of the Agnostina.

Eodiscinids are in many ways ideal subjects for phylogenetic analysis amongst trilobites. They are highly complex morphologically, with a number of unusual character complexes that are likely to be of phylogenetic importance. Most importantly, and in contrast to many groups of Cambrian trilobites, they have generally been well described by authors such as Jell (1975; Bengtson *et al.*, 1990), Öpik (1975), Rasetti (1952, 1966, 1967) and, more recently, Blaker and Peel (1997). The group has recently been extensively reviewed by Jell (1997) and by S. Zhang (*in*

Zhang *et al.*, 1980). The phylogeny of the eodiscinids therefore represents an ideal demonstration of the utility of cladistic methods for resolving the phylogeny of major trilobite groups.

History of eodiscinid classification

In the 19th century all eodiscinid species were included in the genus *Microdiscus* (Emmons 1855), even though at the time the type material was known to be a juvenile post-Cambrian trilobite. Despite this, some attempts were made at subgeneric classification (e.g. Matthew 1896). *Microdiscus* was finally rejected by Raymond (1913), who erected the family Eodiscidae for all eodiscinids. Richter and Richter (1941) followed this monofamilial classification, and argued that blindness may have evolved independently in different lineages within the family. Kobayashi (1935), in contrast, based his taxonomy entirely on this single character and recognised separate families for blind (Eodiscidae) and sighted (Pagetidae) genera. Kobayashi (1943*a*, 1943*b*, 1944) subsequently employed six families (Eodiscidae, Dawsonidae, Weymouthiidae, Dipharidae and Pagetiidae in 1943, adding Hebediscidae in 1944) in a complex classification of the group, which was largely followed by Hupé (1953), who added the Aulacodiscidae but rejected Dipharidae.

Rasetti (1952), reverting to Kobayashi's earlier classification, combined this profusion of families into just two: the Pagetiidae, which included all the eodiscinids with eyes and facial sutures, and the blind and sutureless Eodiscidae. This classification was later also applied to non-American genera (Rasetti *in* Harrington *et al.* 1959). However, Rasetti did not regard his classification as phylogenetic (Rasetti 1952, p. 439): 'in view of the of the incomplete knowledge of the group, it seems expedient to divide the eodiscids into two families....even though such groups may not represent phylogenetic units...the writer agrees with the conclusions reached by R. and E. Richter that the sutureless forms are degenerate descendents of more primitive species with

eyes and facial sutures; it is also likely that eyes and sutures were independently lost in several lines of descent'.

Pokrovskaya (1960) proposed a slightly modified version of Rasetti's scheme with three families: Eodiscidae (without eyes or sutures), Opsidiscidae (with eyes but without sutures) and Pagetiidae (with both eyes and sutures). Subsequently, Russian and Chinese authors have generally followed Pokrovskaya's (1960) classification in the *Osnovy Paleontologii* (e.g. Korobov 1980; Xiang and Zhang 1985) and American and European authors have followed Rasetti's (*in* Harrington *et al.*, 1959) in the *Treatise on Invertebrate Paleontology* (e.g. Rushton 1966; Palmer 1969)

The recognition of the polyphyletic origin of blindness in eodiscinids was first reflected in the classifications of Öpik (1975) and Jell (1975) who, seemingly independently, recognised the families Eodiscidae (a senior synonym of Pagetiidae) and Weymouthiidae for most (Öpik) or all (Jell) eodiscinids. Both authors based their classifications on a wide range of characters. Öpik included both blind and sighted genera in both these families, whereas Jell's Weymouthiidae included only blind taxa. In addition to the Weymouthiidae and Eodiscidae, Öpik recognised the family Calodiscidae for the genera *Calodiscus* and *Neocobboldia.*

Subsequently, Korobov (1980) reverted to Pokrovskaya's classification and J. Zhang (*in* W. Zhang *et al.*, 1980) presented a thorough review of previous classifications and established a complex classification using 12 subfamilies within Pokrovskaya's families.

Most recently, Jell (1997) recognised 6 families, the Tsunyidiscidae, Hebediscidae, Calodiscidae, Yukoniidae, Eodiscidae and Weymouthiidae. He was apparently previously (1975) unaware of W. Zhang's (1966, p. 150) description of *Tsunyidiscus*, and included the Calodiscidae, Hebediscidae and Yukoniidae in the Eodiscidae. In some ways, this classification is a compromise between Jell's (1975) previous classification and that of Öpik (1975), in that the Hebediscidae includes all the sighted taxa included in Öpik's Weymouthiidae. However, this classification was

FIGURE 4.2. History of family-level classification of the Eodiscina. 1: *Stigmadiscus*, 2: *Hebediscina*.

not intended to be entirely natural: Jell (1997, fig. 241) indicated that he regarded most of these families (Tsunyidiscidae, Yukoniidae, Hebediscidae and Weymouthiidae) as paraphyletic.

In conclusion, two distinct classifications of eodiscinids can be recognised. The first, that of Rasetti (1952, 1959), following Kobayashi (1935), and subsequently modified by Pokrovskaya (1960) and S. Zhang (*in* W. Zhang *et al.* 1980), has been used by the vast majority of authors but has never been claimed to represent phylogenetic patterns. In contrast, the second, that of Jell (1975) and Öpik (1975), modified by Jell (1997), has been poorly received but has been supported by phylogenetic arguments. The history of these classification systems is shown in Figure 4.2. Eodiscinid taxonomy is clearly currently unsatisfactory. Cladistic analysis is the only objective way to assess the merits of these previous classifications and provide the basis for the first stable classification of eodiscinids.

Previous phylogenetic hypotheses

Three authors have presented character distribution matrices for eodiscinid taxa in support of supposedly phylogenetic classifications. Jell (1975) used classical phenetic methods to develop a classification of 34 taxa on the basis of 40 characters (Figure 4.3). His 'New Genus 1' and 'New Genus 2' represent *Serrodiscus daedalus* and *Meniscuchus* (both Öpik 1975) respectively (Jell *in* Bengtson *et al.* 1990, p. 259). The resulting classification differed considerably from previous practice by including both sighted and blind forms in both families (Eodiscidae and Weymouthiidae). Öpik (1975, p. 14-15) supported Jell's classification by presenting (*op. cit.*, figure 6) a table of 39 characters coded for 22 eodiscinid taxa, including all the genera that he recognised at the time (Öpik 1975, pp.22-25) and an additional species which he regarded as problematic (*Eodiscus borealis* Westergård 1946, emend. Rushton, 1966). Öpik based his

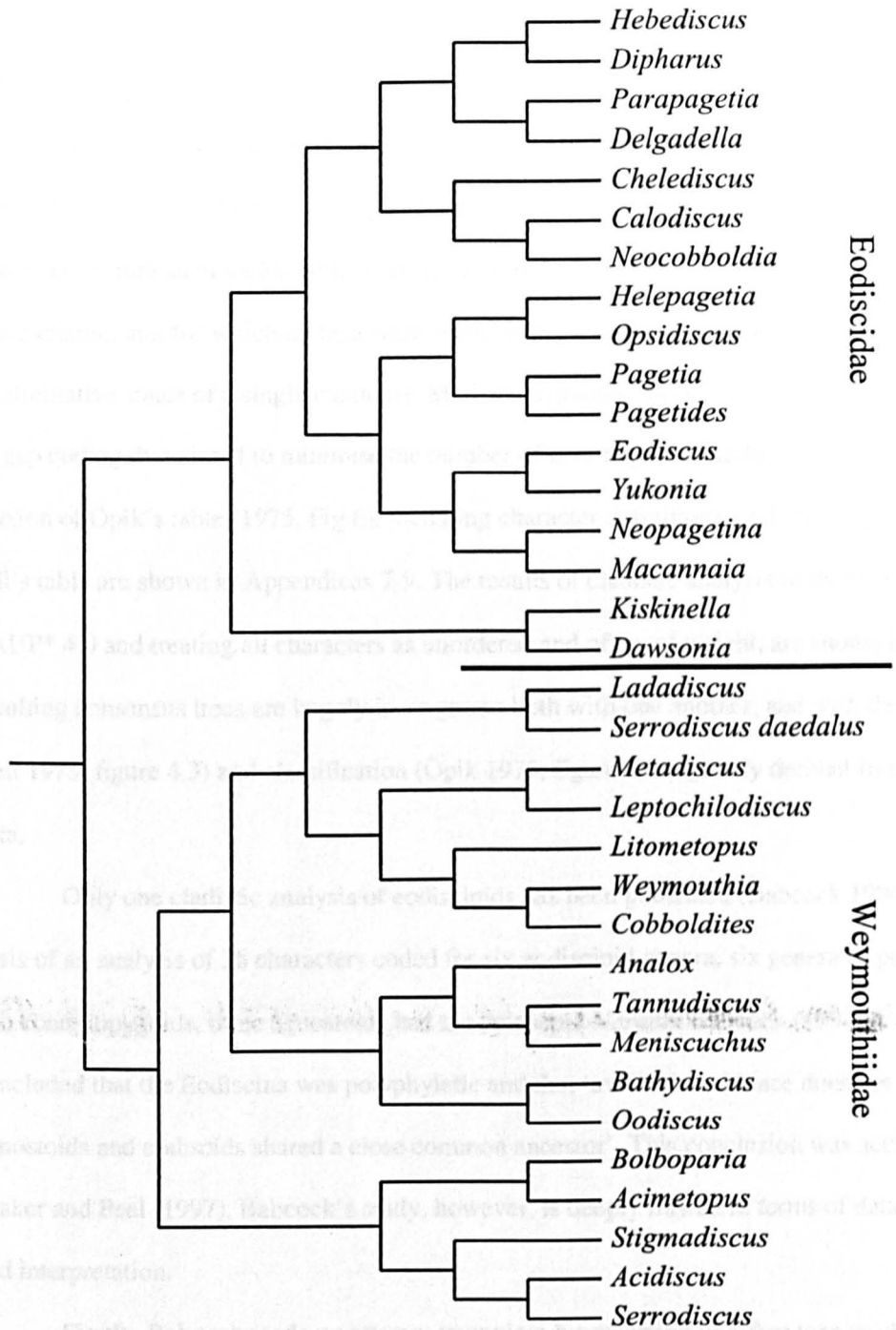


FIGURE 4.3. Original published dendrogram of Jell (1975, text-fig. 5), showing the results of his phenetic analysis of eodiscinid phylogeny.

classification on patterns that he identified subjectively in these data and did not use any numerical method to analyse them.

Both these data matrices were converted to a form amenable to cladistic analysis here (see Appendices 7-9). The majority of Öpik's characters were treated as a single presence/absence character, as indicated on his table. Characters which clearly represent alternative states of the same feature, and for which all taxa were coded as possessing one or the other state, were treated as alternative states of a single character. Meristic characters were coded using an informal version of gap coding that aimed to minimise the number of taxa requiring multiple codings. The recoded version of Öpik's table (1975, Fig.6), including character definitions, and the matrix derived from Jell's table are shown in Appendices 7-9. The results of cladistic analysis of the two datasets, using PAUP* 4.0 and treating all characters as unordered and of equal weight, are shown in Fig. 4.4. The resulting consensus trees are largely incongruent both with one another, and with the dendrogram (Jell 1975, figure 4.3) and classification (Öpik 1975, figure 6) originally derived from the same data.

Only one cladistic analysis of eodiscinids has been published (Babcock 1994). On the basis of an analysis of 26 characters coded for six eodiscinid genera, six genera of polymeroids, two condylopygoids, three agnostoids and the nektaspid *Naraoia* Babcock (1994, p. 112-114) concluded that the Eodiscina was polyphyletic and that 'available evidence does not suggest that agnostoids and eodiscids shared a close common ancestor'. This conclusion was accepted by Blaker and Peel (1997). Babcock's study, however, is deeply flawed in terms of data, methodology and interpretation.

Firstly, Babcock made no attempt to explain his selection of either taxa or characters. Many characters of potential phylogenetic importance are excluded from the matrix. For example, the monophyly of the Corynexochida, from which many of Babcock's polymeroid taxa are drawn (*Olenoides*, *Thoracocare* and *Tonkinella*), is supported by the fusion of the hypostome to the rostral plate (Fortey 1990*b*). Given the small number of characters actually used, excluding this

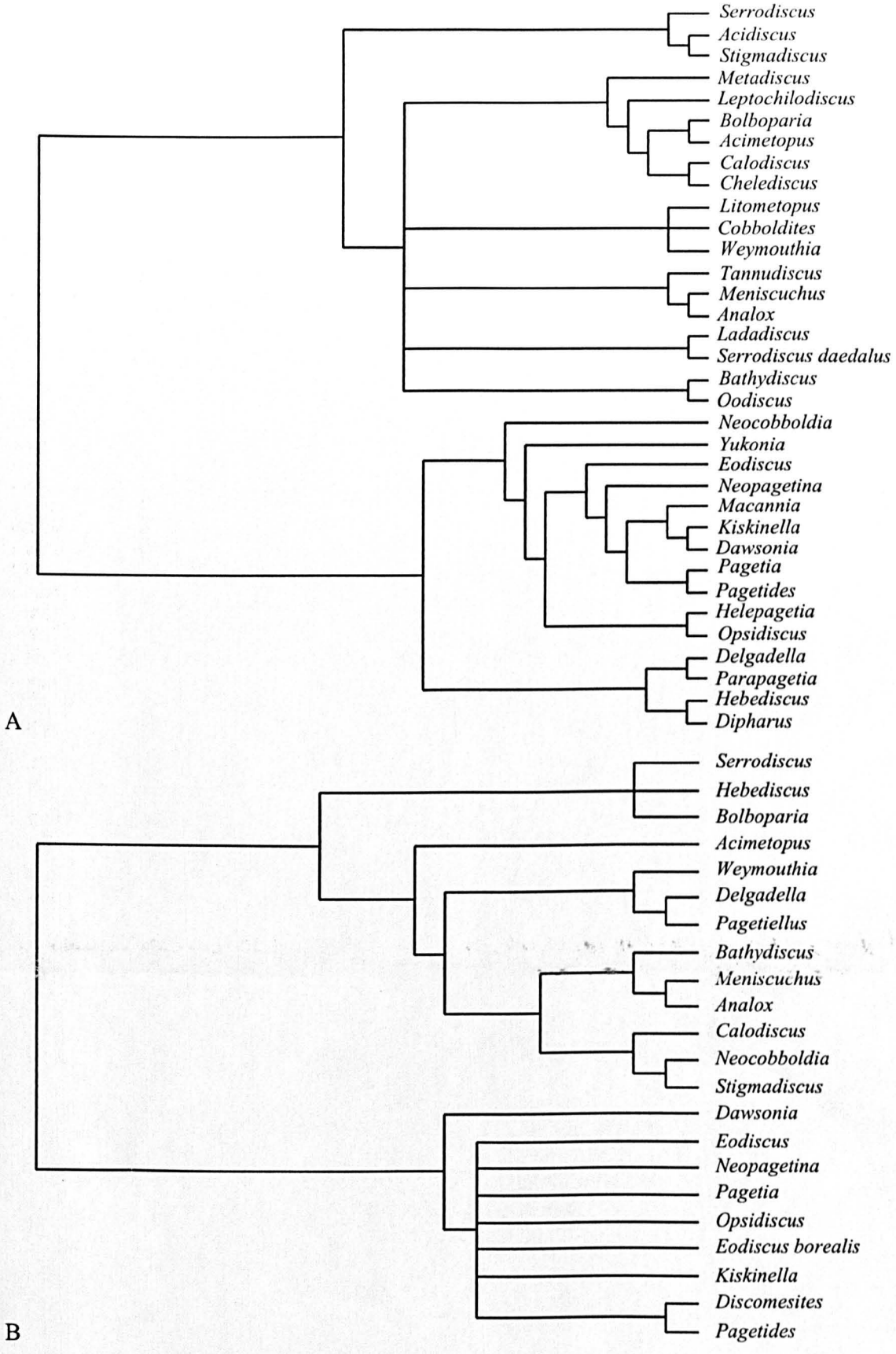


FIGURE 4.4. Strict consensus trees resulting from cladistic analysis of previous character distribution matrices for eodiscinid taxa, treating all characters as unordered and of equal weight and using a heuristic search with 40 addition sequence replicates. A. Consensus of 4 trees of 324 steps resulting from analysis of the matrix shown in Appendix 7 derived from Jell's (1975) Appendix B. B. Consensus of 108 trees of 100 steps resulting from analysis of the matrix shown in Appendix 9 derived from Öpik (1975, fig. 6).

character may have had a considerable impact on the analysis. Babcock included only one of the long list of trilobite synapomorphies presented by Fortey and Whittington (1989): calcification of the exoskeleton. Inclusion of the other characters would result in the exclusion of *Naraoia* from the Trilobita rather than its placement deep within the trilobite clade. Other characters that were included are of doubtful phylogenetic utility. For example, Babcock did not explain why he chose a maximum exoskeletal length of 1 cm as a potential synapomorphy. Similarly, Babcock's choice of taxa is doubtful. His selection of eodiscinids ignores a number of taxa, notably *Tannudiscus* and *Chelediscus*, that have been compared to agnostids by previous authors (Rushton 1966, p. 10; Jell 1975, p. 14). *Serrodiscus* is included in the published matrix but does not appear in the tree supposedly derived from it. No explanation for this is given.

In addition to these problems with the matrix, my re-analysis of the published data generated quite different results to those reported by Babcock (1994). Many more equally parsimonious trees exist than the five that he reported. Treating all characters as unordered yielded 3204 equally parsimonious trees 59 steps long and treating them as ordered, 52 trees 67 steps long (the omission of *Serrodiscus* resulted in 1068 trees 57 steps long or 13 trees of 80 steps, respectively). The majority-rule consensus trees for these analyses (Fig. 4.5) can be compared with Babcock's result (1994, fig. 27). Whilst these consensus trees are broadly similar to Babcock's result, it is clear that he overstated the resolution possible with his data and did not comment on the greater resolution possible when *Serrodiscus* is omitted. Babcock's finding that the agnostoids form a clade to the exclusion of the condylopygoids, polymerids and *Naraoia* is supported by his data, but the sister-group relationship between *Naraoia* and the agnostoids to the exclusion of condylopygoids is not. In the four different analyses I carried out, a closer relationship between *Naraoia* and agnostoids than between condylopygoids and agnostoids was only supported when multistate characters were treated as unordered and then only in 534 of 1068 MPTs with *Serrodiscus* excluded, and in 534 of 3204 MPTs with *Serrodiscus* included. The *Naraoia*–

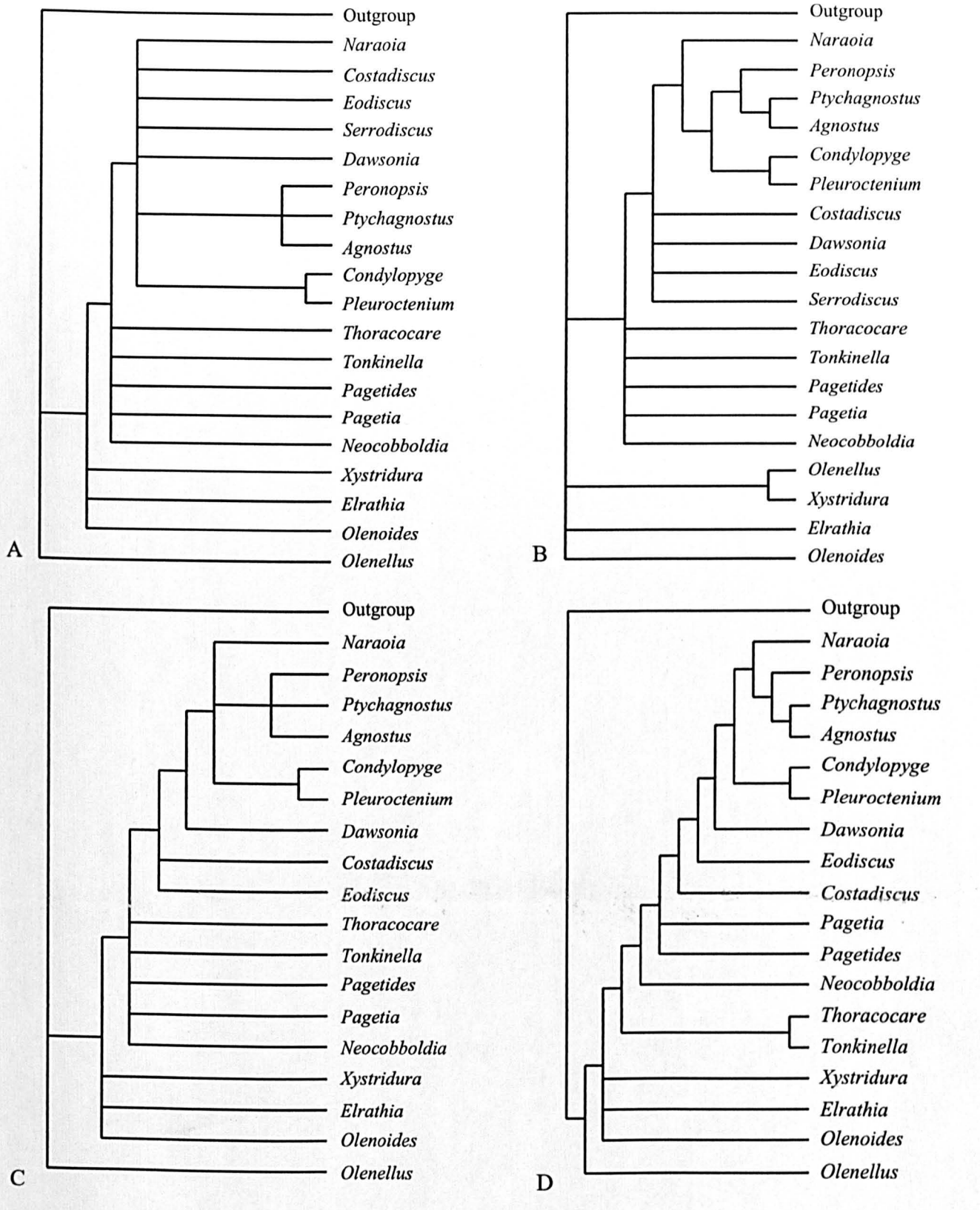


FIGURE 4.5. Majority-rule consensus trees resulting from analysis of Babcock's (1994, pp. 112-114) matrix using heuristic searches with 50 addition sequence replicates. A. Consensus of 3204 trees of 59 steps including *Serrodiscus* and treating all characters as unordered. B. Consensus of 52 trees of 67 steps found with *Serrodiscus* included and multistate characters treated as ordered. C. Consensus of 1068 trees of 57 steps with *Serrodiscus* excluded and all characters unordered. D. Original published cladogram (Babcock, 1994, fig. 27).

agnostoid clade in Babcock's (1994, fig. 27) majority-rule tree therefore seems to represent an error in either his analysis or calculation of the majority-rule tree, and is not supported by his data.

Perhaps most importantly, Babcock's (1994) results, however unreliable, do not support his conclusions. Babcock claims claimed that his results suggest that the eodiscids are 'polyphyletic from trilobites of the order Polymerida'. In fact, on Babcock's tree, the eodiscinids are paraphyletic with respect to a clade including *Naraoia* and agnostids. With the exception of *Naraoia*, which is almost certainly not a trilobite (see above and Edgecombe and Ramsköld 1999), this is exactly the cladistic pattern that would be expected if, as argued here, the agnostids are derived from eodiscinid ancestors and this clade from polymeroids.

In conclusion, none of the three previous attempts to systematically analyse character distribution among eodiscinids has produced a reliable basis for phylogenetic classification of the group. In the case of the studies of Jell and Öpik in 1975, the range of characters included and the methods of analysis were unsatisfactory. Babcock's (1994*a*) cladistic analysis suffers from limitations in the data, errors in the analysis, and incorrect interpretation of the results.

CLADISTIC ANALYSIS

The outline hypothesis of eodiscinid phylogeny identified above on the basis of comparative morphology, and the previous phylogenetic hypotheses of other authors, were tested by cladistic analysis of a matrix of 79 eodiscinid taxa and three agnostids coded for 123 characters. This represents the largest single cladistic analysis of any trilobite group.

Taxonomic sampling

All taxa included in the analysis are listed in Table 8, along with authorship and important subsequent references (including descriptions of other species or genera where these were used during coding). These taxa represent all but one of the eodiscinid genera recognised as valid in the most recent review of the group (Jell 1997). Jell's (1997) taxonomy is followed throughout. None of the material assigned to the Russian and Mongolian genus *Parapagetia* Repina *in* Repina *et al.* 1964 (including *Planodiscus patulus* Korobov 1980) was considered well enough preserved to make coding worthwhile. The material assigned to this genus figured by Jell (*op. cit.*, fig. 243.1a-b) closely resembles *Hebediscus attleborensis.*

Most genera were represented by the type species. In the cases of *Delgadella, Serrodiscus* and *Tannudiscus* the type species was not included. The type species of *Serrodiscus* and *Tannudiscus, S. serratus* Richter and Richter, 1941 and *T. tannuolaicus* Pokroskaya, 1959 respectively, are poorly known compared to other similar species (Rushton 1966; Geyer 1988; Blaker and Peel 1997), *S.speciosus* (Ford, 1873), *T. altus* and *T. balanus*, which were therefore included instead. *Delgadella* is primarily represented in the analysis by *D. caudatus* (Delgado, 1904). The only material assigned to the type species of *Delgadella* Walcott, 1912*a*, *D. lusitanica* (Delgado, 1904), is too poorly preserved to be recognisable as a trilobite - as indicated by its classification as a brachiopod by Walcott (1912*a*). The modern concept of the genus, as employed by Sdzuy (1961, 1962), Geyer (1988) and Jell (1997), is clearly based on the co-occurring eodiscinid specimens described as *Microdiscus caudatus, M. subcaudatus, M. wenceslasi, M. souzai*, and *M. woodwardi* by Delgado (1904), which were all referred to *caudatus* by Richter and Richter (1941). The taxonomy of this group of species is discussed further below.

Most polytypic genera were represented by more than one species, so that the monophyly of genera could be tested and, where supported, generic synapomorphies determined. In most cases, the additional species chosen were the type species of genera considered by Jell (1997) to be

TABLE 8. Authorship and importance references for taxa included in the cladistic analysis of eodiscinid phylogeny. Type species of genera recognised as valid by Jell (1997) are indicated by an asterix (*), type species of genera regarded as junior synonyms are indicated by the name and authorship of the synonymous genus in square brackets.

Agnostina
Condylopyge amitina Rushton, 1966.
Peronopsis roddyi (Resser and Howell, 1938); Blaker and Peel, 1997.
Ptychagnostus gibbus [*Triplagnostus* Howell, 1935] (Linnarsson, 1869); Öpik 1979; Robison 1982; Peng and Robison 2000.
Eodiscina
Abakolia minutus [*Costadiscus* Babcock, 1994*a*] (Babcock, 1994*a*).
*Abakolia pauca** Bognibova *in* Chernysheva, 1971; Korobov 1980; Jell 1997.
*Acidiscus birdi** Rasetti 1966.
Acidiscus theristes Rushton, 1966.
*Acimetopus bilobatus** Rasetti, 1966.
*Alaskadiscus spinosus** (Palmer, 1968); Zhang *et al.* 1980*b*.
*Analox bipunctata** Rasetti, 1966.
*Bathydiscus dolichometopus** Rasetti, 1966.
*Bolboparia superba** Rasetti, 1966.
*Calodiscus lobatus** (Hall, 1847); Lochman 1956; Rasetti 1967; Geyer 1988; Blaker and Peel 1997.
*Cephalopyge notabilis** Geyer, 1988.
*Chelediscus acifer** Rushton, 1966.
Chelediscus chathamensis Rasetti, 1967.
*Cobboldites comleyensis** (Cobbold, 1910); Fletcher 1972 [unpublished]; Jell 1997.
Cobboldites itsariensis Geyer, 1988.
Dawsonia bohemicus [*Aculeodiscus* Šnajdr, 1950] (Šnajdr, 1950); Šnajdr 1958.
*Dawsonia dawsoni** (Hartt *in* Dawson, 1868); Rasetti 1952.
Delgadella caudatus [*Delgadoia* Vogdes, 1917] (Delgado, 1904); Sdzuy 1961, 1962; Geyer 1988; Jell 1997.
Delgadella lenaicus [*Pagetiellus* Lermontova, 1940] (Toll, 1899); Geyer 1988; Jell 1997.
Delgadella amouslekensis [*Pentagonalia* Geyer, 1988] (Geyer, 1988).
*Dicerodiscus tsunyiensis** Zhang, 1964; Zhang *et al.* 1980.
Egyngolia willochra Jell *in* Bengtson *et al.*, 1990.
*Egyngolia obtusa** Korobov, 1980; Jell *in* Bengtson *et al.* 1990; Jell 1997.
Egyngolia zaicevi [*Mongolodiscus* Korobov, 1980] (Korobov, 1980); Jell *in* Bengtson *et al.* 1990.
Ekwipagetia marginata (Rasetti, 1967); Blaker and Peel 1997.
*Ekwipagetia plicofimbria** Fritz, 1973.
Eodiscus borealis Westergård, 1946; Rushton 1966.
*Eodiscus scanicus** (Linnarsson, 1883); Westergård 1946; Rasetti, 1952; Hutchinson 1962; Babcock 1994*a*.
*Hebediscina sardoa** Rasetti, 1972.
Hebediscina blagonravovi (Korobov, 1980); Jell *in* Bengtson *et al.* 1990.
Hebediscina yuqingensis (Zhang, 1980); Jell *in* Bengtson *et al.* 1990.
*Hebediscus attleborensis** (Shaler and Foerste, 1888); Shaw 1950; Hutchinson 1962.
*Helepagetis bitruncula** Jell, 1975.
*Jinghediscus nummularius** Xiang and Zhang, 1985; Jell 1997.
*Kiskinella cristata** Romanenko and Romanenko, 1967; Jell 1997.
*Korobovia ocellata** Jell *in* Bengtson *et al.*, 1990.
*Lenadiscus unicus** Repina *in* Khomentovskii and Repina, 1965; Korobov 1980.
*Leptochilodiscus punculatus** Rasetti, 1966; Rasetti 1967.
Leptochilodiscus succinctus [*Kerberodiscus* Bassett, Owens and Rushton, 1976] (Bassett, Owens and Rushton, 1976); Jell 1997.
*Litometopus longispinus** Rasetti, 1966.

TABLE 8. Continued.

*Luvsanodiscus gammatus** Korobov, 1980; Jell 1997.
*Macannaia maladensis** (Resser, 1939); Rasetti 1966; Jell 1975; Palmer and Halley 1979.
*Mallagnostus desideratus** (Walcott, 1890); Howell 1935; Jell 1997.
Mallagnostus limbatus [*Ladadiscus* Pokrovskaya, 1959] (Pokrovskaya, 1959); Rushton 1966, Jell 1997.
Mallagnostus llarenai (Rushton, 1966); Jell 1997.
*Meniscuchus menetus** Öpik, 1975.
Meniscuchus nanus (Palmer, 1968); Öpik, 1975.
*Natalina incita** Romanenko *in* Repina and Romanenko, 1978; Jell 1997.
Natalina dilata [*Limbadiscus* Korobov, 1980] (Korobov, 1980); Jell 1997.
*Neocobboldia dentata** (Lermontova, 1940); Repina 1972; Jell 1997.
*Neopagetina rjonsnitzkii** (Lermontova, 1940); Jell 1997; Blaker and Peel 1997.
*Ninadiscus strobulatus** Korobov, 1980; Jell 1997.
*Oodiscus subgranulatus** Rasetti, 1966.
*Opsidiscus bilobatus** (Westergård, 1946); Jell 1975; Jell 1997.
Opsidiscus microspinus Jell, 1975.
Opsidiscus longispinus Babcock, 1994*a*.
*Pagetia bootes** Walcott, 1916; Rasetti 1951.
Pagetia prolata Jell, 1975.
*Pagetides elegans** Rasetti, 1945; Blaker and Peel 1997.
Pagetides fragum [*Discomesites* Öpik, 1975] (Öpik, 1975); Jell 1997.
*Pseudocobboldia pulchra** (Hupé, 1953); Geyer 1988.
*Runcinodiscus index** Rushton *in* Bassett, Owens and Rushton, 1976; Jell 1997.
*Semadiscus sollennis** Romanenko *in* Repina and Romanenko, 1978; Jell 1997.
Serrodiscus speciosus [*Paradiscus* Kobayashi, 1943] (Ford, 1873); Rasetti 1952; Lochman 1955; Theokritoff 1964; Blaker and Peel 1997.
Serrodiscus gravestocki Jell *in* Bengtson *et al.*, 1990.
Serrodiscus daedalus Öpik, 1975.
Serrodiscus ctenoa Rushton, 1966.
*Sinodiscus shipaiensis** Zhang *in* Lu *et al.*, 1974; Zhang *in* Zhang *et al.* 1980*b*.
Sinodiscus subquadratus [*Tologoja* Korobov, 1980] (Korobov, 1980); Jell 1997.
*Sinopagetia jinnanensis** Lin and Wu *in* Zhang *et al.*, 1980*b*; Zhang *in* Zhang *et al.*, 1995; Jell 1997.
*Stigmadiscus stenometopus** Rasetti, 1966; Rasetti 1967.
Tannudiscus altus Repina *in* Repina *et al.*, 1964; Rushton 1966.
Tannudiscus balanus Rushton, 1966.
*Tchernyshevioides ninae** Hajrullina *in* Repina, Petrunina and Hajrullina, 1975; Jell 1997.
*Tsunyidiscus niutitangensis** Zhang, 1964; Zhang *et al.* 1980*b*; Jell 1997.
Tsunyidiscus kaiyangensis [*Guizhoudiscus* Zhang *in* Zhang *et al.*, 1980*b*] Zhang *in* Zhang *et al.*, 1980*b*.
Tsunyidiscus aclis [*Mianxiandiscus* Zhang *in* Zhang *et al.* 1980*b*] Zhou, 1975; Zhang *in* Zhang *et al.* 1980 *b*.
Tsunyidiscus orientalis [*Hupeidiscus* Zhang *in* Lu *et al.*, 1974] (Zhang, 1953); Zhang *et al.* 1980 *b*.
Tsunyidiscus longquanensis [*Shizhudiscus* Zhang and Zhu *in* Zhang *et al.*, 1980 *b*] Zhang and Zhu *in* Zhang *et al.*, 1980 *b*; Zhang and Clarkson 1993.
*Weymouthia nobilis** (Ford, 1872); Shaw 1950; Rasetti 1952.
*Yukonia intermedia** Palmer, 1968.
*Yukonides lacrinus** Fritz, 1972; Fritz 1973.

junior synonyms. In addition to type species and species chosen to represent the type (in the cases of *Delgadella*, *Serrodiscus* and *Tannudiscus*), 16 terminals were included in the analyses to represent the range of morphology within polytypic genera as completely as possible. For example, morphological distinctions between *Eodiscus borealis* and the type species of *Eodiscus* were discussed by Öpik (1975) and those between *Serrodiscus daedalus* and *S. gravestocki* and more typical species of *Serrodiscus* by Öpik (1975) and Jell (*in* Bengtson *et al.* 1990). The completeness of material and availability of specimens or English language descriptions were also used as criteria for selecting taxa.

Agnostids were represented by two taxa from the Early Cambrian, the condylopygoid *Condylopyge amitina* Rushton, 1966 and the agnostoid *Peronopsis roddyi* (Resser and Howell, 1938). These species are the earliest occurring and putatively phylogenetically basal (Rushton 1966; Blaker and Peel 1997) members of the two agnostid superfamilies. The ptychagnostid *Ptychagnostus gibbus* (Linnarsson, 1869), was also included in the analysis. The Ptychagnostidae is a diverse and morphologically divergent Cambrian agnostid family and it has been suggested (although this has not subsequently been supported, as far as I am aware) that it may have a separate origin from other agnostids (Jell 1975, text-fig. 6). *P. gibbus* is one of the most widely distributed and thoroughly described Middle Cambrian ptychagnostid and was chosen to represent the family. The position of *P. gibbus* was considered in a cladistic analysis of the Ptychagnostidae by Westrop *et al.* (1996).

Characters and coding

The selected taxa were coded for 123 exoskeletal characters with a total of 299 character states. In total, the database includes 10086 observations (including missing data and inapplicable characters). Characters were based on the hypothesised comparative morphology of eodiscinids

and agnostids presented above and on previous published comparisons of eodiscinid morphology. All characters used in previous studies of eodiscinid phylogeny (including Öpik 1975, Jell 1975 and Babcock 1994) are represented in this study in some form. All characters and character states are described, and some discussed in more detail, in Appendix 10.

The set of characters employed is intended to cover as much as possible of the known morphological variation within the eodiscinids. Variation in the density of character sampling across organ systems or life-history stages therefore reflects differences in the level of known variability between the taxa under consideration, as opposed to investigative or descriptive bias. The 123 characters include 81 cephalic characters, 8 characters of the thorax and 32 characters of the pygidium (2 further characters are concerned with sculpture of the exoskeleton as a whole). This split of characters across organ systems is consistent with the relative paucity of articulated specimens in eodiscinids as a whole and the lack of assigned pygidia for many of the taxa included. The major gap in character construction is the exclusion of characters concerning ontogeny. Growth series are known for very few eodiscinid taxa (reviewed by Chatterton and Speyer 1997), and the inclusion of ontogenetic characters would add little to the analysis.

As discussed in Part Two above, the coding of complex structures in broad cladistic studies presents some particular problems. The approach of coding some characters as 'not applicable', as discussed above, was also employed in this study. Unsurprisingly, given the rather broader range of morphology shown by the eodiscinids than the 'conocoryphids', 'not applicable' codings were used more widely here than in Part Two (1783, or 17.7 per cent of the total number of observations were 'not applicable'). In some instances these form complex nested hierarchies of characters. The conditions under which characters were considered 'not applicable' are listed in Appendix 10.

Character state distributions for all species considered are shown in the matrix in Table 9. Character state assignments were determined primarily on the basis of published descriptions and illustrations. Major references used for the coding of each taxon are listed in Table 8. This reliance

TABLE 9. Data matrix used in phylogenetic analyses of Agnostida. The full names of taxa are used on the first pages of the matrix. Subsequently taxa are referred to by six letter codes. and Character numbers are shown at the top of the table; characters and states are described in Appendix 10. Missing data are indicated by a question mark, 'N' refers to non-applicable characters. Other capital letters indicate multistate uncertainty coding, as follows: A = {01} (126 instances), B = {12} (88 instances), C = {23} (54 instances), D = {34} (20), E = {45} (1), F = {56} (1), G = {67} (3), H = {78} (2), I = {89} (2), J = {012} (1), K = {123} (2), L = {234} (1), M = {678} (1).

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Taxon	Code	Character number 1111111111222222222233333333334444444445 12345678901234567890123456789012345678901234567890
Condylopyge amitina	ConAmi	0000N000NN00NNNNN00010N0N0103101010N000011NNNNNNNN
Peronopsis roddyi	PerRod	1NN0NA00NN00NNNNN00000N0N1103101A10N000011NNNNNNNN
Ptychagnostus gibbus	PtyGib	0010NA00NN00NNNNN00000N0N0103101011200011NNNNNNNN
Abakolia minutus	AbaMin	1NN0NA010200NNNNN000B0N1100010000111001011NNNNNNNN
Abakolia pauca	AbaPau	1NN0NA00NN00NNNNN000C1110000A0000110000011NNNNNNNN
Acidiscus birdi	AciBir	00011200NN01120000010N1100030000010N000011NNNNNNNN
Acidiscus theristes	AciThe	00111200NN01110000020N1000030000010N000011NNNNNNNN
Acimetopus bilobatus	AcmBil	0000N200NN00NNNNN000B0N1000030000010N000011NNNNNNNN
Alaskadiscus spinosus.	AlaSpi	1NN0NA00NN00NNNNN00000N0N000100020NN0000000002C200
Analox bipunctata	AnaBip	1NN0NA00NN00NNNNN001413???00300?00NN001111NNNNNNNN
Bathydiscus dolichometopus	BatDol	0100NA00NN00NNNNN000110N010310000NN000011NNNNNNNN
Bolboparia superba	BolSup	0000N200NN0100020?00212???002000011000111NNNNNNNN
Calodiscus lobatus	CalLob	1NN0N000NN00NNNNN00010N0N000B000B0NN00001????00301
Cephalopyge notabilis	CepNot	1NN0NA00NN00NNNNN001??????10B000?10N000?11NNNNNNNN
Chelediscus acifer	CheAci	0000N2011000NNNNN00000N0N010C00101120000011NNNNNNNN
Chelediscus chathamensis	CheCha	00?0NA011100NNNNN00010N0N010C00101120000011NNNNNNNN
Cobboldites comleyensis	CobCom	1NN0NA00NN00NNNNN00010N1000010000NN000011NNNNNNNN
Cobboldites itsariensis	CobIts	1NN0NA00NN00NNNNN000A0N10000B00000NN000011NNNNNNNN
Dawsonia bohemicus	DawBoh	1NN0NA012200NNNNN00020N1000010000NN001011NNNNNNNN
Dawsonia dawsoni	DawDaw	1NN0NA012200NNNNN00030N10000B00000NN001011NNNNNNNN
Delgadella caudatus	DelCau	1NN0NA00NN00NNNNN000A0N1200030001100000011N23B00
Delgadella lenticus	DelLen	1NN0NA00NN00NNNNN00000N1000020001100000011N1?100
Delgadella amouslekensis	DelAmo	1NN0NA00NN00NNNNN00000N0N0001000110N00000011N1?100
Dicerodiscus tsunyiensis	DicTsu	1NN10A00NN00NNNNN00030N1100001002ONN000010100101O1
Egyngolia willochra	EgyWil	1NN0NA00NN00NNNNN000211110001000111100100000001B0?
Egyngolia obtusa	EgyObt	1NN0NA00NN00NNNNN00000N10000J000B11100100000000201
Egyngolia zaicevi	EgyZai	1NN0NA00NN00NNNNN00000N0N0002000211100?011NNNNNNNN
Ekwipagetia marginata	EkwMar	1NN0NA00NN10NNNNN00020N1000020001ONN0010001001CA00
Ekwipagetia plicofimbria	EkwPli	1NN0NA00NN10NNNNN00020N0N100C00010NN001000100B2000
Eodiscus borealis	EodBor	1NN0NA012B00NNNNN00010N1000020001112001011NNNNNNN0
Eodiscus scanicus	EodSca	A000NA010100NNNNN00000N0N000B0001112001011NNNNNNN0
Hebediscina sardoa	HbiSar	1NN0NA00NN00NNNNN0002101000OC00020NN00000000021100
Hebediscina blagonravovi	HbiBla	1NN0NA00NN00NNNNN000A0N0N?00B000211?0010001?0B?C00
Hebediscina yuqingensis	HbiYuq	1NN0NA0???00NNNNN000C1011000200011100010001OOAB100
Hebediscus attleborensis	HbsAtt	1NN0NA00NN00NNNNN00020N120003???10NN00000001N112?1
Helepagetis bitruncula	HelBit	1NN0NA011100NNNNN00000N0N100B1000110001010llN1DA00
Jinghediscus nummularius	JinNum	1NN0NA0110010?020000A0N0N1003001010N100011NNNNNNNN
Kiskinella cristata	KisCri	1NN0NA012200NNNNN00040N1200010000110001000101111OO
Korobovia ocellata	KorOce	1NN0NA00NN00NNNNN00010N0N000B00020NN00100000001301
Lenadiscus unicus	LenUni	0000NA00NN00NNNNN00010N10000C000010N0100000?010011
Leptochilodiscus punculatus	LepPun	1NN0NA10NN00NNNNN00000N0N101C100010N000011NNNNNNNN

Page 2/4		Character number
Taxon	Code	1111111111222222222233333333334444444445 12345678901234567890123456789012345678901234567890
Leptochilodiscus succinctus	LepSuc	1NN0NA10NN010?02000000N0N100C10000NN000111NNNNNNNN
Litometopus longispinus	LitLon	0010N200NN00NNNNN00020N11010100000NN000011NNNNNNNN
Luvsanodiscus gammatus	LuvGam	1NN0NA00NN00NNNNN00010N11000200020NN00000011N22100
Macannaia maladensis	MacMal	1NN0NA010200NNNNN000B0N11000C00011120010011N1D100
Mallagnostus desideratus	MalDes	1NN0NA00NN00NNNNN00010N???003001010N100011NNNNNNNN
Mallagnostus limbatus	MalLim	1NN0NA00NN00NNNNN00010N0N100C001110N100011NNNNNNNN
Mallagnostus llarenai	MalLla	1NN0NA00NN0112020000B0N0N000C001010N000011NNNNNNNN
Meniscuchus menetus	MenMen	1NN0NA00NN00NNNNN010C0N11000201000NN001111NNNNNNNN
Meniscuchus nanus	MenNan	1NN0NA00NN00NNNNN0102111200030100ONN001111NNNNNNNN
Natalina incita	NatInc	1NN0NA00NN00NNNNN00041210000 3?0?11100010001001?100
Natalina dilata	NatDil	1NN0NA00NN00NNNNN00021110000C00011100010011N1?100
Neocobboldia dentata	NeDen	1NN0NA00NN00NNNNN00000N1200020002ONN00?000?0011100
Neopagetina rjonsnitzkii	NepRjo	1NN0NA010200NNNNN000B12110001000111100100010D200
Ninadiscus strobulatus	NinStr	1NN0NA00NN0101101100D1112000B00000NN001111NNNNNNNN
Oodiscus subgranulatus	OodSub	01010200NN00NNNNN00000N0N0103100010N000011NNNNNNNN
Opsidiscus bilobatus	OpsBil	1NN0NA011100NNNNN000A0N0N1001100011A001010?1012B10
Opsidiscus microspinus	OpsMic	1NN0NA011B00NNNNN00010N110001100011B0010101102?110
Opsidiscus longispinus	OpsLon	1NN0NA00NN00NNNNN00000N0N1000100011000101001010B10
Pagetia bootes	PagBoo	1NN0NA011200NNNNN00020N1000020000112001000110?100
Pagetia prolata	PagPro	1NN0N0011210NNNNN000B0N1100010000111001000110131OO
Pagetides elegans	PdsEle	1NN0N0010200NNNNN000C1111000C00011110010001001DA00
Pagetides fragum	PdsFra	1NN0NA010B00NNNNN00021111000 2000A11000100011N11B00
Pseudocobboldia pulchra	PsePul	1NN0NA00NN00NNNNN00020N1100010001ONN00001000000200
Runcinodiscus index	RunInd	1NN0NA00NN011200000000N10000300011ON000011NNNNNNNN
Semadiscus sollennis	SemSol	1NN0NA00NN00NNNNN00020N120002000110N000011NNNNNNNN
Serrodiscus speciosus	SerSpe	1NN0NA00NN013B01000020N120002000A10N000011NNNNNNNN
Serrodiscus gravestocki	SerGra	1NN0NA00NN012111000020N1100030001ONN000011NNNNNNNN
Serrodiscus daedalus	SerDae	1NN0NA00NN0120100100C0N1100020010100000011NNNNNNNN
Serrodiscus ctenoa	SerCte	0000N100NN01120010001ON0N000200000NN000011NNNNNNNN
Sinodiscus shipaiensis	SinShi	1NN0NA00NN00NNNNN00000N0N000100010NN00000000011301
Sinodiscus subquadratus	SinSub	1NN0NA00NN00NNNNN00000N0N000100010NN00000000022301
Sinopagetia jinnanensis	SpaJin	1NN0NA011200NNNNN00030N1200020000110001000110 2?200
Stigmadiscus stenometopus	StiSte	0100NA00NN00NNNNN00010N1000010000 10N000011NNNNNNNN
Tannudiscus altus	TanAlt	1NN0NA00NN00NNNNN000A0N0N010C001010N000011NNNNNNNN
Tannudiscus balanus	TanBal	0100N100NN00NNNNN000111ON110310100NN000011NNNNNNNN
Tchernyshevioides ninae	TchNin	0010NA00NN00NNNNN0002100N000000000NN00000000011301
Tsunyidiscus niutitangensis	TsuNiu	0000NA00NN11B00001002ON0N0001000010N00000010015200
Tsunyidiscus kaiyangensis	TsuKai	0000NA00NN11?0000?002ON0N0002000010N00000010025100
Tsunyidiscus aclis	TsuAcl	0010NA00NN11C01001002ON0N0002000A10N00000011N25200
Tsunyidiscus orientalis	TsuOri	0000NA00NN00NNNNN000A0N1000030001 10N00000010025000
Tsunyidiscus longquanensis	TsuLon	1NN0N000NN00NNNNN000B100N0001000010N00000010025200
Weymouthia nobilis	WeyNob	1NN0NA00NN0112?2000010N100003000A?0N000011NNNNNNNN
Yukonia intermedia	YuiInt	1NN0NA00NN00NNNNN00000N0N00000001ONN00101000100301
Yukonides lacrinus	YudLac	1NN0NA011000NNNNN000A0N0N0002000B0NN00001000100200

	Character number
	111111111111111111111111
Code	555555555666666666677777777778888888888999999999900000000001111111111222
	123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890123
ConAmi	0NCC0120N000010N011001002N000110N10030100N000004100?1111?0N01N10000111001
PerRod	0NB20120N000000N011000002N100110N00020000N000004100?0111?0N01N10000111011
PtyGib	0N2B0120N000000N011000002N1101110100200000N000003100?001110N01N10000111101
AbaMin	0NB1012201?0001000?000001N1101010001100000N000000000050000NNN10010000000000
AbaPau	11C10122?100001000?000001N100A?????220000N00000A000D0000NNN10010000??000?
AciBir	0N22001AN0N0110N001000010N0001?????0A000101000020008000NNN11N10000??000?
AciThe	0NB20000N0N0110N001000010N00010??100B0001010000B000H0001?0N11N10000000000
AcmBil	0N320120N000100N00110020210001?????000000N00000300150011100N01N10001??000?
AlaSpi	1122012200100010000010?0N100110N00210001100000210OC11?110N00210000000000
AnaBip	0N3B0120N001100N00110010110000?????000000N11000C00050010NNN01N11010??000?
BatDol	0N4C010200N0000N000001010N1002?????0B0000N111004100?1010NNN01N10000??000?
BolSup	0NB20000N0N0100N001000000N1100?????000001010000200090001O0N01N11001??000?
CalLob	11CB0000N0N0000N100000A0A0?0010????1C000110000030000B0000NNN00010000000000
CepNot	0NB31100N0N2000N000001010N100000N00001000N000014010?1010NNN01N10010000000
CheAci	0N120120N000000N010001002N110010N00000000N110004000C0010NNN11N10000000000
CheCha	0NB20120N0000?0N01?001001N1100???????0?00N11000300020010NNN11N10000??000?
CobCom	0N430?0???N2000N?00001010N10000????100000N00000D01041110NNN01N11010000000
CobIts	0NDC0100N0NB000N000001010N1001?????000000N000003010?10?0NNN01N11000??000?
DawBoh	0N2101220?0000110000000?0N110A1????210000N000003001200O0NNN00010001000000
DawDaw	0N2101220?0000110000000?0N110110N00110000N000001001300O0NNN00010001000000
DelCau	0N?31?0???N2?00N?00001010N?11A00N00010000N000011000?1000NNN01N10000000000
DelLen	0N331000N0N2000N100001010N011000N00010000N00001?00071000NNN01N11000000000
DelAmo	0N331?0???N2?00N?00001010N0110?????010000N00001C000?1000NNN01N10000??000?
DicTsu	10220000N0NB010N10?0010?0N1110???????0000N00000??000???0NNN?00?0000??000?
EgyWil	111B012211100011000010001N1011?????2B000110000010003O000NNN10200000??000?
EgyObt	11AB01221110001?00?010001N101100N?0220000N00000A00030000NNN1000?000000000
EgyZai	11A10122111000??00?010001N?011?????????????????????????????????00????0?
EkwMar	11B2012200100010000000000N1?01?????B10001100000C000201011200020000O??000?
EkwPli	111B012200100010000000000N1001?????110001100000C000110011200020000O??000?
EodBor	0N1101220??0001000?000000N110100N10A10000N00000A00030000NNN10010000000000
EodSca	0NA1012201000010000000000AN11010??00AA0000N00000A000M0000NNN11N1001000000
HbiSar	20B1012201000010000000000N1001?????0B000110000OC00020000NNN1010000??000?
HbiBla	1011012200100001?00?00000?N1001?????130001100000A00020000NNN1?2?0000??000?
HbiYuq	11B10122?100001100000000N1001?????020001100000200040000NNN10100000??000?
HbsAtt	B0230000N0N2010N000001010N1011??????20000N00001?010?10?0NNN01N10000??000?
HelBit	0N2B012200000010000000001N1101?????B10000N000002001000012211011000I??000?
JinNum	0NA20120N001000N00?00?002N0000?????030100N000004100I1010NNN01N10000??000?
KisCri	1131012200?000??000001010N1000?????010000N000001001300O0NNN00010000??000?
KorOce	11210000N0N0000N100001002N1001?????130001100000D00010000NNN10010100??000?
LenUni	2000012??0?0001000000????N0001?????1C0010N00000C10010100NNN01N10000??000?
LepPun	0N320100N0N0000N100001010N0101?????000001010010D000G1110NNN01N11010??000?
LepSuc	0N4C1100N0N0110N000001010N110110N00000001010011D000I1010NNN11N11010000000
LitLon	0N420101N0N0000N000001010N0001?????1A000101100030000?1010NNN01N10010??000?
LuvGam	102C0000N0N1010N100000000N101100N00A2000110000020004010ONNN00101000000000
MacMal	11B101221?100011000000000N11011110012000ON000001001301011201020000000000
MalDes	0N020?0???N2?00N000001010N1001?????0??????????????????????????????00????0?
MalLim	0N110100N0N0000N00?001010N10010????030100N00000C10070010NNN01N10000??000?
MalLla	0N120100N0N0000N001000000N1001?????030100N00000C?00H0010NNN11N10000000000
MenMen	A1320122000000O0N00100020200000?????010000N11100D01140000NNN11N10000??000?
MenNan	0N3201220000000N00?00010100000?????000000N???00401040000NNN11N10000??000?
NatInc	??2B000A?0NB?00N100001010N1001?????030000N000001010D0000NNN?0B10000??000?

Page 4/4	Character number
	11111111111111111111111
Code	55555555566666666667777777777888888888899999999990000000000111111111122222
	12345678901234567890123456789012345678901234567890123456789012345678901234567890123
NatDil	101B0??2????00N?00001010N1001?????130000N000002000300000NNN??2?0000??000?
NeDen	0N120000N0N0000N100001010N101100N?023000110000030000A0000NNN01N10000000000
NepRjo	1121012211000011000000001N1?01?????110000N000000000400000NNN10000000??000?
NinStr	0N3B0120N000000N00?00010201000?????00000?0??000B00170000NNN11N11000??000?
OodSub	0N33012BN000000N000001010N1002?????020000N000003100?1010NNN01N10000??000?
OpsBil	111101220??0001000?000002N1101?????AB0000N000001000B0000NNN10110000??000?
OpsMic	11B1012200000010000000001N110111100B10000N000001000100000NNN10110000000000
OpsLon	1110012200000010000001002N1002??????????????????????????????????????00????0?
PagBoo	1112012200000010000000001N11011110011000N000001001C000122101N10000000000
PagPro	1111012200000010000000001N11011110011000N00000A00?B000122110200000000000
PdsEle	112B012211000011000000001N1101?1100A10000N000001000400000NNN10200000000000
PdsFra	112B012210000011000000000N1101?????110000N000001000300000NNN10000000??000?
PsePul	103B0000N0N0000N000001010N1000?????B20001100000C?0000100NNN002?0000??000?
RunInd	0N331100N0N2000N000001010N0000?????000001010001400OG1010NNN01N11000??000?
SemSol	0N320100N0N0010N000001010N0001??????????????????????????????????????00????0?
SerSpe	0N320100N0N1000N0000001?A0000000N000100011100003000G0000NNN11N10000000000
SerGra	0N32012AN000000N00110020200000?????000001110000D000F00?100N?1N1?000??000?
SerDae	0NCB01220000000N00110020200000?????020100N00000?00070000NNN?1N10000??000?
SerCte	0ND20100N0NB000N000001010N000100N0000000111000D0005011ONNN01N11000000000
SinShi	20310000N0N0000N0000002020000000N00120000N00000D10010000NNN00000001000000
SinSub	20CB0000N0N0000N0000002020000 1?????130000N00000D10010000NNN00000000??000?
SpaJin	1?2201220000000N000001010N1000?????010000N000001000200000NNN01N10000??000?
StiSte	0N2B0111N0N0110N001010000N0001??????0?01110000 3???90011?1N10010000??000?
TanAlt	0NCC0120N000000N00?000002N0001?????030100N00000C000?1000NNN01N10000??000?
TanBal	0NC30120N000000N001001002N000100N10030100N00000D000E0110NNN01N10000000000
TchNin	20320000N0N0010N100000000N1000?????2B0000N00000A0003000ONNN00010000??000?
TsuNiu	1?200120N010000N00110010100000000N00220000N000000100D1000NNN00010000000000
TsuKai	1?C1012??01B000N001100A010000000N00B10000N000000100C1000NNN10210000000000
TsuAcl	1?20012??011000N001100A0100001?????000001100000000040100NNN?0210000000000
TsuOri	1?210120N010000N00110010100000000N00110000N000000100K0000NNN11N10000000000
TsuLon	0NC1012AN011000N00110010100000000N00210001100000010040100NNN000100000000000
WeyNeb	0N??1?0???N???0N?00001010N??0?00N?002000??????1?????10?0NNN01N10000000000
Yaifni	11B101220000001000000101ON110100NC12C0001100000B100K0101?0N00B0000000000C0
YudLac	111101221100001?000000000N1001?????A20001100000B100L0000NNN10200000??000?

on literature was necessary given the very broad scope of this study, both taxonomically and geographically. Coding from the literature was supplemented by examination of specimens in the collections of the Natural History Museum (London), the Sedgwick Museum (University of Cambridge), the National Museum of Natural History (Smithsonian Institution, Washington DC) and the large collection of casts, including taxa from China and Russia, of the Institute for Cambrian Studies (Boulder, Colorado).

Of the 123 characters employed, eight (characters 31, 42, 91, 94, 96, 122, 128 and 129) are autapomorphic. These were included in the character list and character distribution matrix for completeness - to provide a comprehensive database of eodiscinid morphology as a basis for further work. Cladistically uninformative characters were excluded from all analyses and are not included in the calculation of any tree statistics.

The broad taxonomic scope of this study, and the approach taken in selecting terminals, resulted in the inclusion of many taxa that are incompletely known, poorly preserved and little studied. Combined with the conservative approach taken to coding, this resulted in a total of 10.7 per cent of the total observations being either missing data or multistate uncertainty coding.

Methods

These data were subjected to cladistic analysis using the software package PAUP* version 4 (Swofford 1999), beta test version 8 for Windows or version 6 for MacOS. All searches used a heuristic search algorithm with starting trees constructed by a random stepwise addition sequence. The number of addition sequence replicates used varied across different analytical conditions according to the complexity of the analyses.

Initial analysis treated all characters as unordered and of equal weight and treated 'not applicable' characters as equivalent to missing data. Other analyses were carried out to investigate the effect of these assumptions. Firstly, 'not applicable' codings were treated as a distinct character

state. Secondly, 24 characters coding continuous features (Characters 9, 10, 12, 14, 21, 23, 25, 29, 33, 36, 46, 47, 48, 51, 53, 54, 62, 73, 75, 86, 86, 98, 102 and 112) were treated as ordered. Thirdly, this set of characters was treated as ordered and weighted so that the total weight of these characters was equal to that for discrete characters. The conditions used for each of these analyses are summarised in Table 10. The treatment of continuous and 'not applicable' characters is discussed in more detail in Part Two.

Bremer support and bootstrap values were calculated for all nodes in analysis 1. Bootstrap values were based on 200 bootstrap replicates, each consisting of 5 addition sequence replicate heuristic searches. Bremer support values were calculated on the basis of 20 addition sequence replicate heuristic searches.

Whilst it is generally accepted that eodiscinids evolved from polymerid trilobites by paedomorphosis (Stubblefield 1936, Jell 1975, Fortey 1990, Shergold 1991) the sister-group of the Agnostida within the Trilobita is unclear. Outgroup rooting was therefore not considered appropriate for this analysis. Instead, all analyses were unrooted. The resulting trees were rooted by treating the Tsunyidiscidae (consisting only of the genus *Tsunyidiscus*, following the recent revision of Jell (1997) as a monophyletic sister-group to all other taxa. *Tsunyidiscus* is the earliest known eodiscinid and shows a number of features (Jell *op. cit.*, p. 384) that are likely to be primitive for eodiscinids based on comparison with juvenile redlichioids (Fortey 1990). These include the narrow glabella with well defined dorsal furrows, well defined eye ridges and palpebral lobes, and the furrowed pygidial pleurae. Whether the tsuniyidiscids are paraphyletic with respect to other Agnostida (Jell *op. cit.*, fig. 241) or a monophyletic sister-group to them has no impact on their use for rooting the trees produced here provided that the remaining members of the Agnostida form a monophyletic group.

Results

The results of the three analyses carried out, in terms of the number and length of MPTs retrieved and a range of popular tree statistics, are shown in Table 10.

The initial analysis, treating all characters as unordered and equally weighted and 'not applicable' characters as missing data, found 72 MPTs each 1119 steps long. The strict consensus of these trees, along with selected bootstrap and bremer support indices, is shown in Figure 4.6. Clade numbers and letters referring to paraphyletic assemblages used below are shown on this figure. The same set of MPTs was obtained in 3 of the 30 addition sequence replicates, so it is unlikely that shorter trees exist. In the strict consensus tree, the majority of species fall into two major sister clades, clades 1 and 2 of Fig. 4.6, containing 40 and 34 of the 85 taxa analysed respectively. Other ingroup taxa formed a paraphyletic group (group a of Fig. 4.6) basal to these large clades, consisting of *Calodiscus* and *Korobovia*, *Tchernyshevioides*, a monophyletic *Sinodiscus*, and *Lenadiscus unicus* as successive sister-taxa to remaining ingroup Agnostida.

The larger of the two major clades (clade 1 of Fig. 4.6) included a subclade (clade 3) containing all taxa assigned by Jell (1997) to the family Weymouthiidae with the exception of *Abakolia*, along with *Chelediscus* and the agnostids. Within the broader clade (1), *Hebediscus attleborensis*, a monophyletic *Delgadella* and *Neocobboldia dentata* (group b of fig. 4.6) formed successive outgroups to the weymouthiid, *Chelediscus* and agnostid clade (3). This latter clade comprised three groups. A *Cephalopyge*, *Weymouthia* and *Runcinodiscus* clade, a monophyletic *Cobboldia* and a *Bathydiscus* and *Oodiscus* clade formed a basal paraphyletic group (group c) to a clade (clade 4) made up of two large subclades. The first of these (clade 5) contained the weymouthiid genera *Analox*, *Ninadiscus*, *Meniscuchus*, *Acimetopus*, *Acidiscus*, *Bolboparia*, *Stigmadiscus*, *Semadiscus*, *Leptochilodiscus* and *Litometopus*, and species of *Serrodiscus* arranged polyphyletically. The second clade (clade 6) consisted of the weymouthiids *Tannudiscus*, *Mallagnostus* and *Jinghediscus*, *Chelediscus* and the agnostids. Within clade 6, *Mallagnostus*

TABLE 10. Details of cladistic analysis conditions and results. Columns show, from left to right, a numerical code identifying each analysis, the treatment of 'not applicable' (N/A) character codes ('Missing' as missing data or 'Add. state' as an additional character state), treatment of continuous characters (whether ordered and/or reweighted in separate columns), the number of addition sequence replicates used in the heuristic search, the number of most parsimonious trees (MPTs) found, the number of addition sequence replicates in which trees of minimum length were found, the length of MPTs and the consistency index (CI), rescaled consistency index (RCI) and retention index (RI) of MPTs.

Analysis	N/A chars	Cont. chars ordered	Cont. chars reweight.	Add. seq. reps	No. MPTs	Reps hit	MPT Length	CI	RCI	RI
1	Missing	N	N	30	72	3	1119	0.423	0.257	0.609
2	Add. state	N	N	100	1365	14	1304	0.388	0.245	0.632
3	Missing	Y	Y	500	12	3	821.5	0.328	0.204	0.633

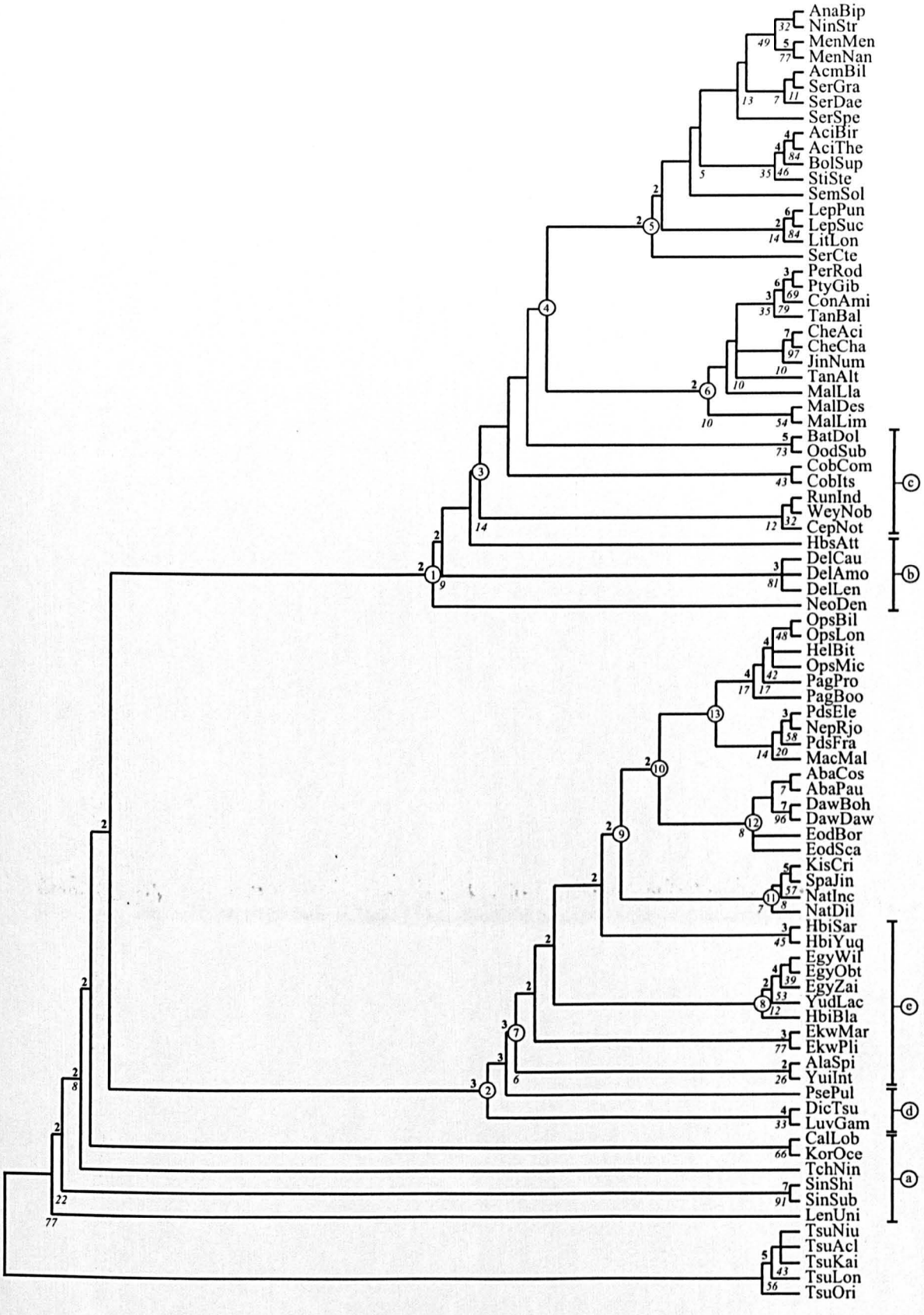

FIGURE 4.6. Strict consensus of 72 trees of 1119 steps resulting from analysis 1 (see Table 11) of the matrix shown in Table 9.Taxa are referred to by the six letter codes shown in Table 9. Clades and paraphyletic assemblages referred to in the text are indicated by numbers over nodes and lower case letters in circles, respectively. Bootstrap percentages based on 200 bootstrap replicates each of 5 addition sequence replicates are shown in italics below each node where the value was greater than 5%. Bremer support values are shown above nodes in bold type, for all nodes with a support value greater than 1.

formed a basal paraphyletic assemblage to an unresolved trichotomy involving *Tannudiscus altus*, a *Jinghediscus* and *Chelediscus* clade and a *Tannudiscus balanus* and agnostid clade. Within the agnostids, the condylopygoid *Condylopyge amitina* was found to be the sister-group to the agnostoids *Peronopsis* and *Ptychagnostus*.

The smaller of the main clades found in analysis 1 (clade 2 of fig. 4.6) contained all the taxa assigned by Jell (1997) to the Eodiscidae and Yukoniidae, with the exception of *Lenadiscus unicus* (placed in Yukoniidae by Jell), alongside *Abakolia* (Weymouthiidae), *Pseudocobboldia* (Calodiscidae), *Dicerodiscus*, *Natalina*, *Neopagetina* and *Luvsanodiscus* (Hebediscidae). *Pseudocobboldia* and a *Dicerodiscus* and *Luvsanodiscus* clade (collectively group d of Fig. 4.6) formed successive outgroups to all other taxa (clade 7). The Yukoniidae formed a paraphyletic basal group (group e) to a clade consisting largely of Eodiscidae (clade 9) within clade 7. Within this yukoniid assemblage, a clade of *Hebediscina sardoa* and *H. yuqingensis*, a clade consisting of *H. blagonravovi*, *Yukonides* and a monophyletic *Egyngolia* (clade 8), an *Ekwipagetia* clade and an *Alaskadiscus* and *Yukonia* clade formed four successive outgroups to clade 9. Within clade 9, *Kiskinella*, *Sinopagetia* and a paraphyletic *Natalina* constituted the sister-group (clade 11) to all other taxa (clade 10). Clade 10 consisted of a clade (Clade 12) containing *Abakolia*, *Dawsonia* and *Eodiscus* in opposition to a clade (Clade 13) containing *Pagetia*, *Opsidiscus*, *Helepagetic*, *Pagetides*, *Neopagetina* and *Macannaia*.

The second analysis, in which 'not applicable' codings were treated as a distinct character state but conditions otherwise kept as in the first analysis, found 1365 MPTs each 1304 steps long (Table 10). The strict consensus of these trees (Fig. 4.7) is not well resolved but is largely compatible with that found in the first analysis. The ingroup taxa form two large clades and a large unresolved group. The first large clade consists of the Weymouthiidae, agnostids and a few other taxa, identical to the constituents of clade 3 in the first analysis (Table 11). The second major clade contains the Eodiscidae, Yukoniidae and a few other taxa, as found in clade 7 of Fig. 4.6. The basal group consists of the most basal paraphlyetic assemblage from the first analysis (group a),

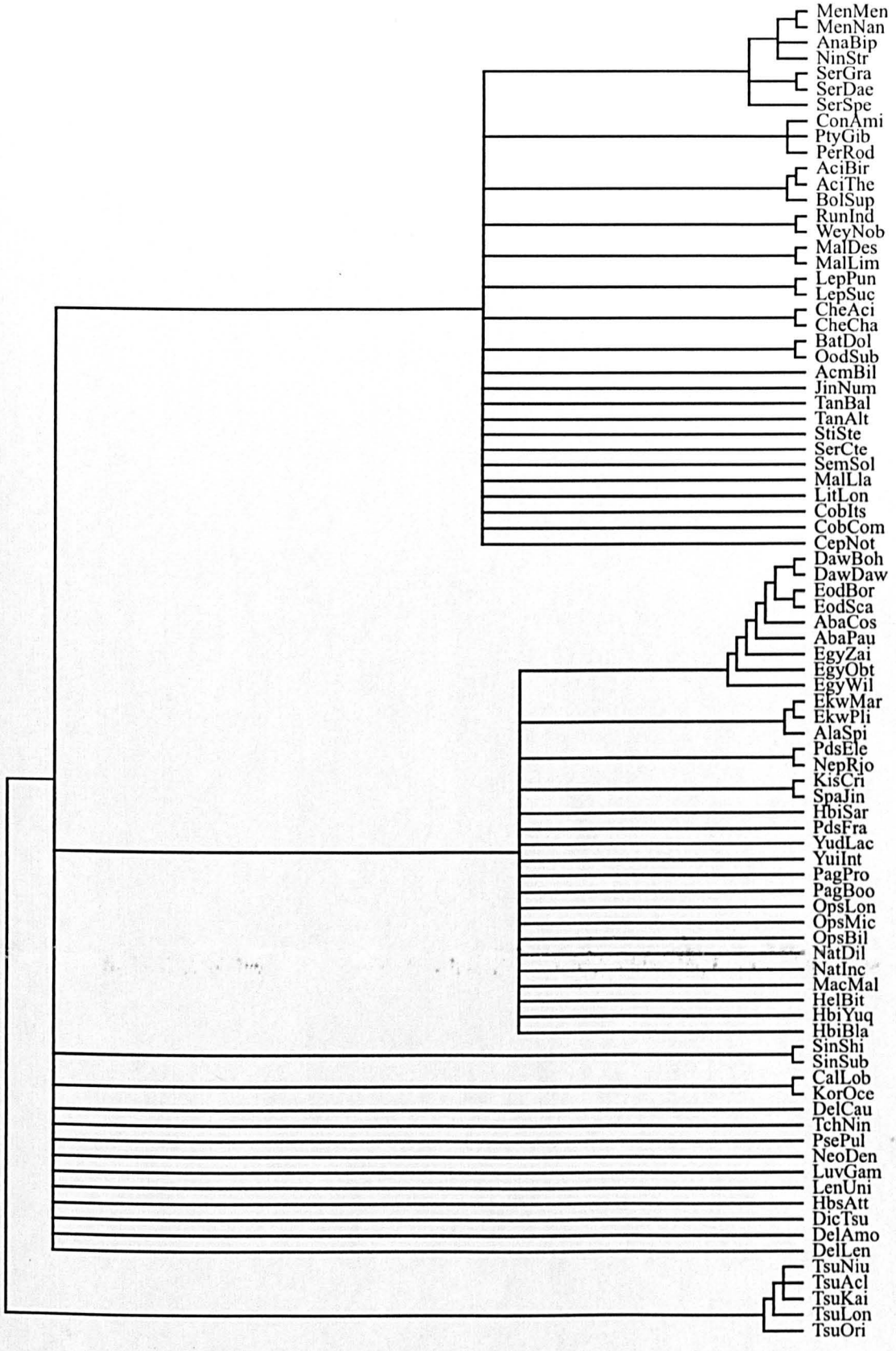

FIGURE 4.7. Strict consensus of 1365 trees of 1304 steps resulting from analysis 2 (see Table 11) of the matrix shown in Table 9. Taxa are referred to by the six letter codes shown in Table 9.

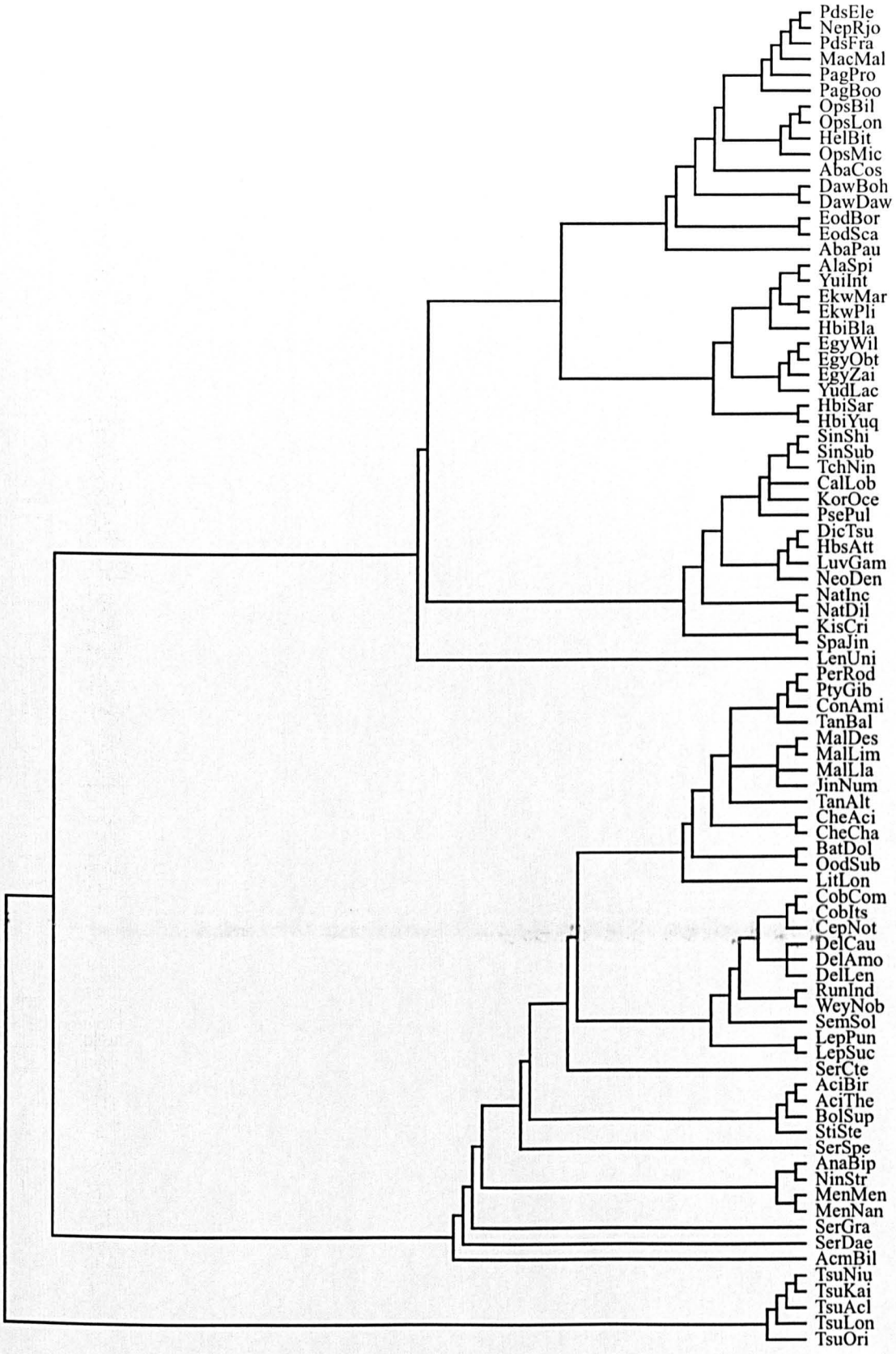

FIGURE 4.8. Strict consensus of 12 trees of 821.5 steps resulting from analysis 3 (see Table 11) of the matrix shown in Table 9.Taxa are referred to by the six letter codes shown in Table 9.

plus the taxa forming basal assemblages in both the major clades (clades 1 and 2; groups b and d respectively). The results of the second analysis are thus largely compatible with those of the first.

The results of the third analysis, when a set of continuous characters were ordered and reweighted, are less compatible with those of the first analysis. This third analysis resulted in 12 MPTs 821.5 steps long (Table 10). The strict consensus of these trees is shown in Fig. 4.8. The status of the major groups identified on this tree is shown in Table 11. In third analysis, all taxa except tsunyidiscinids fell into two sister-groups of approximately equal size. The first of these consisted of the same taxa (weymouthiids, *Chelediscus* and agnostids) as clade 3 in the first analysis, with the addition of a monophyletic *Delgadella*. However, the arrangement of taxa within this clade differed. The *Chelediscus*, *Jinghediscus*, *Mallagnostus*, *Tannudiscus* and agnostid subclade (clade 6) was still supported and nested deeply within the larger weymouthiid clade. This group now form the sister-group to a clade containing largely taxa that formed the basal assemblage (group c) of clade 3 in the first analysis. Members of the other main subclade (clade 5) in the first analysis now largely form a paraphyletic assemblage with respect to the other members of the weymouthiid clade (clade 3). Thus the positions of clade 5 and group c with respect to clade 6 have been largely reversed compared to the first analysis.

In the first analysis, taxa assigned by Jell to the Hebediscidae and Calodiscidae were distributed amongst assemblages that were basal to the non-tsunyidiscid Agnostida as a whole (group a), the broad eodiscid + yukoniid clade (group d) and the weymouthiid + agnostid clade (group b). In the third analysis these taxa largely form a major subclade, along with *Natalina*, *Kiskinella* and *Sinopagetia* (clade 11 in Fig. 4.6), in opposition to an eodiscid + yukoniid clade. The eodiscid + yukoniid clade differs in content from that in the first analysis (clade 7) only through exclusion of these three genera. However, the arrangement of taxa within this clade is rather different. In analysis 1, the yukoniids formed a large paraphyletic assemblage with respect to an Eodiscidae + *Abakolia* clade (clade 9). The yukoniids now formed a monophyletic sister-group to clade 9. Within this clade, *Abakolia*, *Dawsonia* and *Eodiscus* (clade 12) formed a

TABLE 11. Status of the clades and paraphyletic assemblages identified on the strict consensus tree resulting from the first analysis, see Fig. 4.6, on the strict consensus trees resulting from the second and third analyses. Question marks indicate groups whose status is ambiguous due to lack of resolution.

Group from analysis 1	Status from analysis 2	Status from analysis 3
Clade 1	?	Polyphyletic
Clade 2	?	Polyphyletic
Clade 3	Monophyletic	Monophyletic with addition of *Delgadella*
Clade 4	?	Paraphyletic with addition of *Delg.* and Group c
Clade 5	?	Paraphyletic
Clade 6	?	Monophyletic
Clade 7	Monophyletic	Paraphyletic
Clade 8	Not monophyletic	Paraphyletic
Clade 9	?	Paraphyletic
Clade 10	?	Monophyletic
Clade 11	?	Paraphyletic
Clade 12	Monophyletic	Paraphyletic
Clade 13	?	Monophyletic
Group a	?	Monophyletic with exclusion of *Lenadiscus*
Group b	?	Polyphyletic
Group c	?	Polyphyletic
Group d	?	Polyphyletic
Group e	?	Monophyletic

paraphyletic assemblage with respect to a clade (clade 13) consisting of *Helepagetia*, *Macannaia*, *Neopagetina*, *Opsidiscus*, *Pagetia* and *Pagetides*, rather than the sister-group to it.

DISCUSSION

The considerable number of differences between the results from the two analyses with well resolved results (i.e. the first and third of the analyses described above) shows that the topology supported by the data is highly sensitive to *a priori* assumptions about character evolution. Unfortunately, the data were difficult and extremely time consuming to analyse, and the scope for investigating a wider range of combinations of assumptions consequently limited.

The results of the first analysis are the preferred hypothesis and, except where otherwise stated, form the basis for the discussion presented here. This analysis made minimal assumptions about character evolution. There is no *a priori* evidence that transitions in any of the characters that were ordered and re-weighted in the third analysis always or usually involved passing through intermediate stages. Processes such as heterochrony, which is thought to have been common amongst Cambrian trilobites (McNamara 1981, 1986), could have allowed evolutionary transitions from one state of a continuous character to another state without passing through intermediate states. Secondly, at the taxonomic level of this study it is a reasonable *a priori* assumption that the presence or absence of discrete features provides a better guide to phylogeny than morphometric similarities. The set of continuous characters had a greater influence on topology in analysis 3 than in the preferred analysis.

The results from analysis 1 suggest that the assumption that *Tsunyidiscus*, which was used to root the trees, is the sister-group to other Agnostida , did not introduce significant bias. Other taxa that have been considered basal within the Eodiscina are closely related to (but do not form a clade with) *Tsunyidiscus*. Fortey (1990, p. 556), for example, suggested that *Sinodiscus*

changyanensis S. Zhang *in* Zhang *et al.*, 1980 could be the most primitive eodiscinid. *S. changyanensis* was not included in this analysis. However, rooting using either or both the species of *Sinodiscus* that were included would have produced similar results to rooting using *Tsunyidiscus*. Similarly the genera *Hebediscus* and *Neocobboldia*, suggested as basal members of two of the three eodiscinid lineages identified by Jell (1975, text-fig. 6), , were found to be basal in this analysis. Hence, rooting using either of these genera would have had little impact on the topology of the trees presented here.

The analysis confirms much of Jell's (1997, fig. 241) phylogeny. Like Jell this study suggests that the Yukoniidae is paraphyletic with respect to Eodiscidae and the Weymouthiidae with respect to Agnostina. However, Jell's suggestions that the Calodiscidae forms a third major monophyletic lineage and that the Hebediscidae is paraphyletic with respect to the weymouthiid + agnostid clade are not supported. Instead, taxa assigned by Jell to Hebediscidae and Calodiscidae were intermingled in three paraphyletic groups – at the base of all Agnostida except Tsunyidiscidae, and at the base of the Eodiscidae + Yukoniidae clade and Weymouthiidae + Agnostina clade.

The results presented here disagree more strongly with other previous studies of eodiscinid phylogeny. Only 2 of the 28 comparable nodes on Jell's (1975) tree based on phenetic analysis (Figure 4.3) are supported by this analysis. Some of this disagreement is due to differences in analytical methodology: 9 of the 17 comparable nodes in the strict consensus tree (Fig. 4.4A) resulting from the cladistic analysis of Jell's data are supported by this study. Comparatively few of the results (Fig. 4.4B) of my cladistic analysis (3 out of 14 nodes) of Öpik's (1975, figure 10) character distribution table are supported by this study. This is probably due to the much narrower range of characters employed by Öpik than by Jell. Finally, the results supported here are strongly at odds with those of Babcock (1994). Of the published hypothesis (Babcock 1994*a*, fig. 27, reproduced as Fig. 5.5D herein), only the nodes uniting *Peronopsis* and *Ptychagnostus*, and uniting this clade with *Condylopyge*, are supported here.

The origin of agnostids

This analysis strongly supports the hypothesis, developed on the basis of comparative morphology, that agnostids are derived from a clade of weymouthiid eodiscinids. All analyses found the agnostids to be monophyletic and nested within a clade including the eodiscinid genera *Mallagnostus*, *Chelediscus*, *Tannudiscus* and *Jinghediscus*. This group was also universally found to be part of a wider weymouthiid clade. The shortest trees in which the three agnostid taxa did not form a clade with the derived weymouthiids listed above were 7 steps longer than the MPTs.

Patterns of character evolution were mapped onto one of the 72 MPTs resulting from the first analysis. The chosen MPT (shown in Figure 4.9) was one of nine that were compatible with the 50% majority-rule consensus tree, which showed *Opsidiscus microspinus* as the sister-group to a clade including *Helepagetia bitruncula*, *Opsidiscus bilobatus*, and *Opsidiscus longispinus* (supported by 75% of MPTs), *Eodiscus* as a monophlyetic sister-group to a *Dawsonia* + *Abakolia* clade (50% of MPTs), and *Tannudiscus altus* as the sister-group to the clade combining *T. balanus* and agnostids (50% of MPTs). The other two clades that were unresolved in the strict consensus tree (trichotomies involving *Tsunyidiscus aclis*, *T. kaijiangensis* and *T. niutitangensis*, and *Delgadella amouslekensis*, *D. caudatus* and *D. lenaicus*) were randomly resolved. Apomorphies mapped onto the chosen tree using the accelerated transformation optimisation criterion (Kitching *et al.* 1998, p. 72-73, see above) are listed in Appendix 11 and shown in Figure 4.9.

The cladistic analysis does not provide a sufficiently robust hypothesis to justify detailed investigation of the pattern of morphological evolution during the origin of the agnostids. The results, however, provide no support for the hypothesis that the origin of the agnostid body-plan involved an unusual evolutionary event. Firstly, the pattern of reconstructed branch lengths suggests that branches leading to the agnostid clade are not unusually long or short compared to

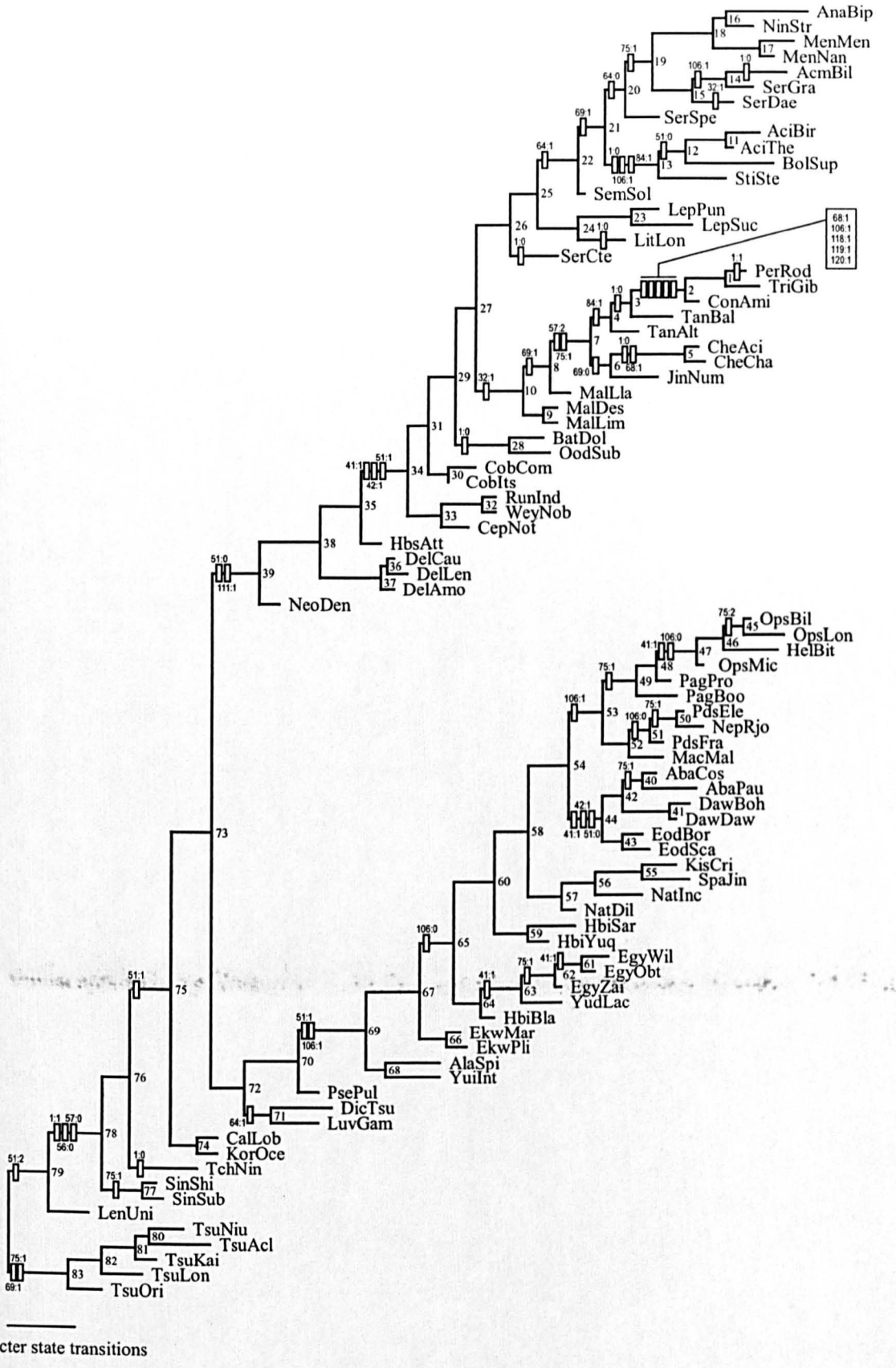

FIGURE 4.9. One of 9 of the 72 MPTs from analysis 1 that are compatible with the 50% majority-rule consensus tree, showing reconstructing character state transitions. Node numbers, immediately to the right of nodes, refer to a detailed list of apomorphies in Appendix 11. Taxa are referred to using six letter codes listed in Table 9. Reconstructed changes in characters discussed in the Comparative Morphology section of the text are shown as boxes over internal branches, labelled with the character number and apomorphic state (e.g. boxes labelled 1:0 show a transition to state 0 in character 1).

other branches. Figure 4.10 compares the reconstructed lengths of all internal branches to their distance, in terms of branches, from the root. Branches connecting directly to the root and terminal branches were excluded since their length is determined more by rooting assumptions and the selective inclusion of autapomorphies than by the data. Analysis of variance using the software package SPSS for Windows (v. 10.0.5) showed no statistical relationship between depth in the tree and branch length, either for the entire set of data ($R^2 = 0.023$, $p = 0.169$) or for branches along the lineage leading to the agnostids ($R^2 = 0.073$, $p = 0.262$). The branch immediately subtending the agnostids could not be distinguished statistically from this distribution, with a standardised residual of 1.545 standard deviations from the regression line. Observations within 2 standard deviations of the regression line are expected to contain 95% of values, assuming a normal distribution (Pagano 1998).

This result must, however, be considered somewhat tentative pending further analysis of the phylogeny of the Agnostida in terms of refining the analysis presented here and extending the database to include a greater range of taxa and characters. A number of biases will also have affected these results. Comparison of cladistic branch lengths assumes that taxonomic sampling is comparable throughout the tree. This effect has received little attention in previous studies using a similar approach (e.g. Wagner 1995, 1997). There is no compelling reason to suppose that this is the case here. Secondly, the method used for measuring hierarchical depth is strongly influenced by tree balance.

This analysis provides no evidence that the number of morphological innovations in the origin of the agnostids was unusual, nor is there any evidence that the morphological innovations themselves were generally distinctive. As shown in Figure 3.9, many of the major morphological features defining the agnostid body plan are widely distributed amongst the eodiscinids, and a number are broadly convergent throughout the Agnostida. Only three characters are uniquely derived in the agnostids. These are the loss of segmentation of the posterior part of the pygidial axis, division of the thoracic axis into median and lateral lobes, and loss of the articulating half-

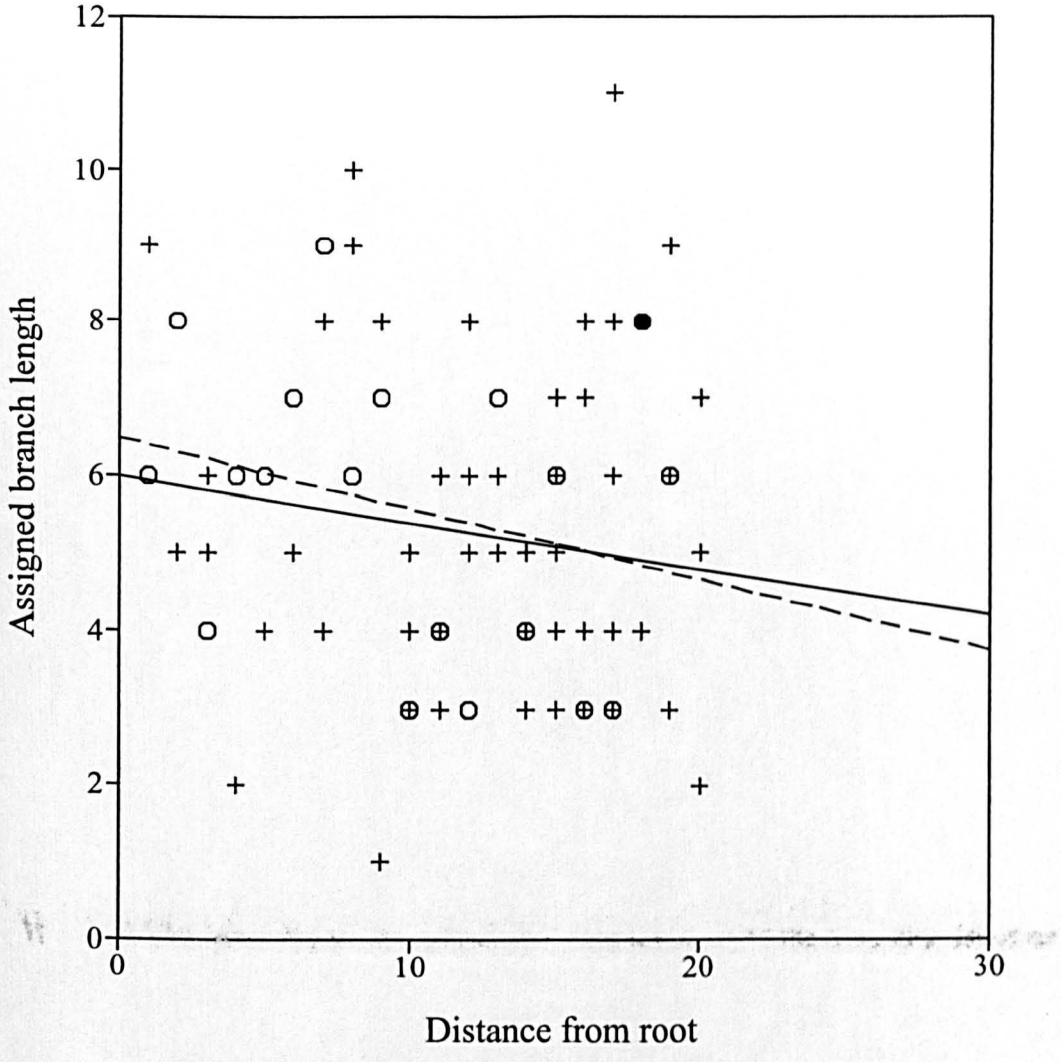

FIGURE 4.10. Distribution of internal branch lengths on the chosen tree shown in Figure 4.9. Circles represent branches leading directly to the Agnostina, crosses represent all other branches. The branch immediately subtending the Agnostina (i.e. connecting nodes 2 and 3 of Figure 4.9) is shown by a filled circle. Best-fit lines from linear regression are shown for the whole sample (unbroken line) and for branches leading to the Agnostina separately (dashed line). Regression statistics: For all observations, R-squared = 0.023, p = 0.169; for the agnostid lineage, R-squared = 0.073, p = 0.262.

ring of the first thoracic segment. I am aware of no suggestion that these characters represent major morphological or developmental innovations.

If agnostids do indeed fit the pattern of evolution during the Cambrian explosion suggested by Gould (1989, 1991), which can only be confirmed when phylogeny within the Agnostina is better understood, this study suggests that explanations involving unusual cladogenetic events (see Foote 1996) are unlikely. Instead, the pattern may have been caused by an increased rate of phylogenesis during the origin of the group, or by constraints acting during subsequent evolution. Evidence against the former, based on cladistic revision of another Early Cambrian trilobite clade (Lieberman 1999*b*), has recently been presented (Lieberman 2001). A more complete understanding of the evolution of the agnostid body plan will, in addition to improvements in the robustness of the present analysis, require extension of this work to include a full range of taxa within the Agnostina and the integration of stratigraphic data.

Systematics of the Agnostida

This study clearly has important implications for the taxonomy of the Agnostida. However, detailed taxonomic considerations are outside the scope of this work, and formal taxonomic revision would be somewhat premature given the lack of robustness of the phylogenetic results. In general, the results presented here support the multi-character classifications of Öpik (1975) and Jell (1975), and strongly reject the alternative view (e.g. Pokrovsyaka 1960; Korobov 1980; Zhang *et al.* 1980) that blind and sutureless eodiscinids form a distinct lineage to sighted taxa.

The results of this study do not allow significant improvements to be made to Jell's (1997) family-level classification. Whilst few of Jell's families emerged as monophyletic groups on the preferred tree, the results are insufficiently well supported to provide a sound basis for a familial revision. Instead, their paraphyly should be acknowledged using Wiley's (1979) quotes

convention. However, the families Calodiscidae (Kobayashi 1943, p. 48) and Hebediscidae did not form separate groupings in any analysis and, in the preferred tree, formed a broad basal paraphylum with respect to all non-tsunyidiscid taxa. The separation of these two basal families by Jell is therefore rejected here and they should be combined under the earlier name Calodiscidae pending further investigation. This emended 'Calodiscidae' is characterised by the plesiomorphic retention of a vertical occipital ring, strongly defined and relatively wide palpebral lobes, a glabella that is at least a quarter of the width of the cephalon, and pygidial pleural furrows.

Three genera should be reassigned, based on this analysis. As discussed above, *Chelediscus* is better placed in the 'Weymouthiidae' than in the Calodiscidae. Conversely, Jell (1997, p. 392) placed *Abakolia* in his Weymouthiidae whereas in the cladistic analysis, it was found to be deeply nested within the Eodiscidae. The genus *Natalina* should also be re-assigned to the Eodiscidae, from the Hebediscidae where Jell (*op. cit.*, p. 389) placed it.

More significantly, the primary conclusion of this work, that the eodiscinids are paraphyletic with respect to agnostids, deserves to be recognised taxonomically. This is a difficult problem, given that the use of the Order Agnostida for the clade including both groups and the Suborder Agnostina for the clade comprising the agnostoids and condylopygoids is well established. Furthermore this taxonomy is likely to be widely used following its adoption in the recent revision of the trilobite volume of the *Treatise on Invertebrate Paleontology* (Kaesler, 1997). Inflating the rank of the Order would seem unwise given the widespread use and relative stability of the ordinal classification of trilobites as a whole. Instead, revisions to taxonomy at the Suborder level to reflect the phylogeny of the Agnostida are proposed.

The two major clades recognised above are here recognised as an emended Eodiscina and Agnostina. The name Agnostina is proposed for the grouping of the 'Weymouthiidae', the Agnostoidea and Condylopygoidea, and the Eodiscina for the 'Yukoniidae' and Eodiscidae. The monophyly of both these groups is strongly supported by the analysis. Members of the Eodiscina share the synapomorphies of a glabella extended posterodorsally over the occipital ring, an

incomplete occipital furrow, a long and narrow pygidial axis, and a narrow pygidial border. The Agnostina, as revised here, is characterised by the loss of eyes and facial sutures, a posteriorly angled occipital ring with retention of a complete occipital furrow, and the loss of pygidial pleural furrows,. The infraorder name Agnostini is available for the agnostids as conventionally recognised – the clade combining the Agnostoidea and Condylopygoidea. Pending further investigation the Tsunyidiscidae and Calodiscidae can be recognised as a paraphyletic 'Calodiscina', consisting of Agnostida lacking the synapomorphies of other suborders. The classification of the Agnostida proposed here is shown in Figure 4.11, alongside the most recent classification (Jell 1997, Fortey 1997).

In his recent review, Jell (1997) synonymised a number of eodiscinid genera without comment. Most of these suggestions are supported here. Representatives of the genera *Tologoja* (type species *T. subquadrata* Korobov 1980, p. 81) and *Mongolodiscus* (type species *M. zaicevi* Korobov 1980, p. 99) erected by Korobov (1980) on the basis of Mongolian material were found to be closely related to the type species of the genera *Sinodiscus* and *Egyngolia*, respectively, to which Jell (1997) assigned them. Jell's synonymy of *Costadiscus* Babcock, 1994 with *Abakolia* Korobov, 1980 and of *Kerberodiscus* Bassett, Owens and Rushton, 1976 with *Leptochilodiscus* Rasetti, 1966 is also supported. Jell's separation of *Neopagetina* Pokrovskaya, 1960 and *Pagetides* Rasetti, 1945 at the family-level is not supported. Rather, as Blaker and Peel (1997) argued, these genera are better regarded as synonyms. Finally, Jell (1997, p. 388-389) suggested that the genera *Pagetiellus* Lermontova, 1940 and *Pentagonalia* Geyer, 1988 should be regarded as synonyms of *Delgadella* Walcott, 1912*a*. Representatives of these three genera formed a well-supported clade in all analyses. However, the genus *Delgadella* is based on material too poorly preserved to be recognisable as a trilobite, much less an eodiscinid – as evidenced by Walcott's (*op. cit.*, p. 560) description of the genus as a brachiopod. The name *Delgadella* should therefore be restricted to the type material of *Lingulepis lusitanica* Delgado, 1904. The next available name for other material referred to *Delgadella* is *Delgadoia* Vogdes, 1917 (type species *Microdiscus caudatus* Delgado,

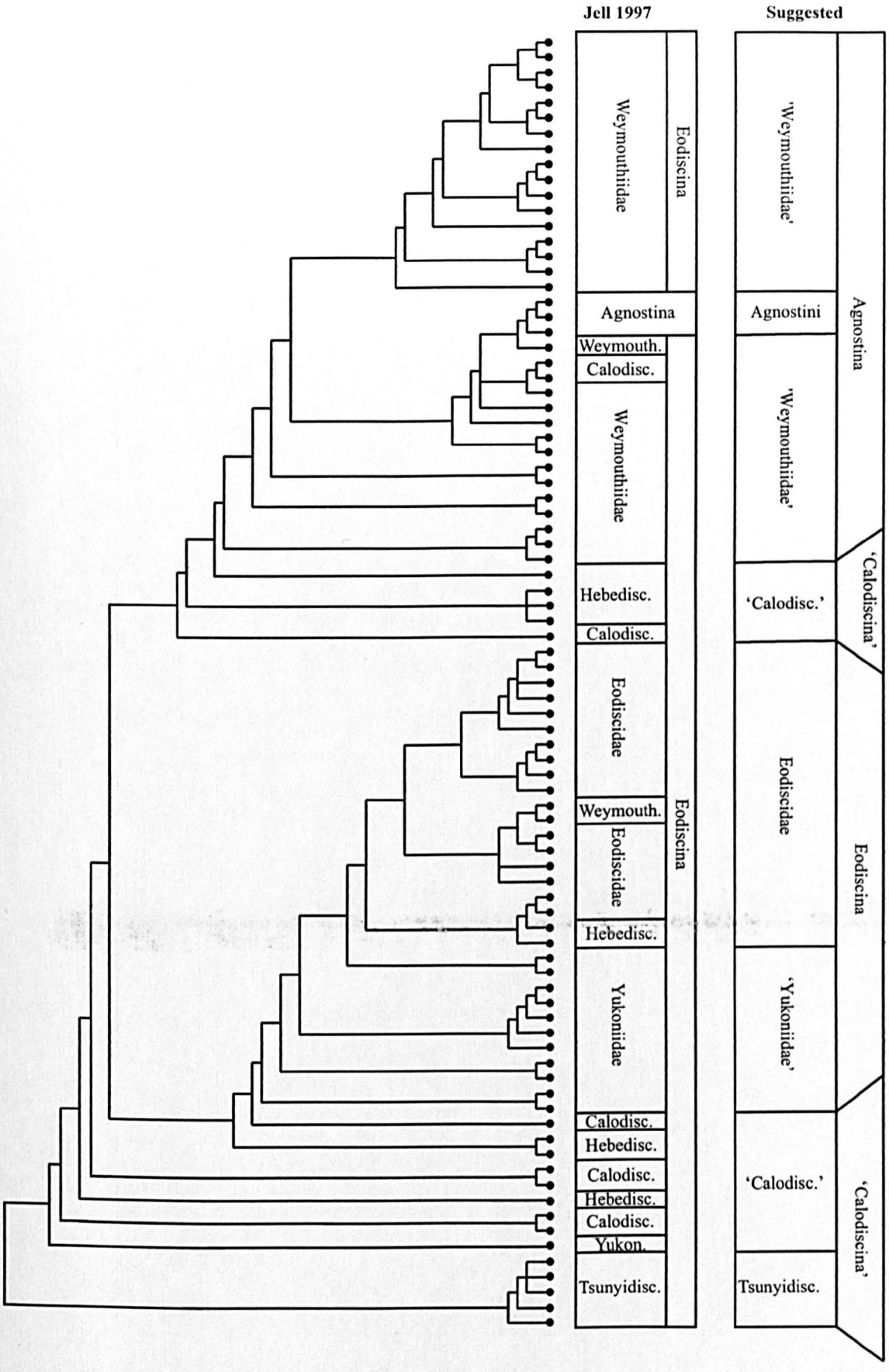

FIGURE 4.11. Comparison of Jell's (1997) classification of eodiscinid taxa included in this study and the preliminary taxonomic revision suggested here. See text for details.

1904). The genera *Alemtejoia* Kobayashi, 1935 (type species *Microdiscus souzai* Delgado, 1904), *Pagetiellus* Lermontova, 1940 (type species *Microdiscus lenaicus* Toll, 1899) and *Pentagonalia* Geyer, 1988 (type species *P. amouslekensis* Geyer, 1988) are therefore here regarded as subjective junior synonyms, and *Delgadodiscus* Kobayashi, 1935 (type species *Microdiscus caudatus* Delgado, 1904) as an objective synonym, of *Delgadoia*.

A number of genera are unlikely to be monophyletic and are in need of revision. Firstly, *Serrodiscus* emerged as polyphyletic in all analyses. This conclusion was also supported by the data presented by Jell (1975; see Figures 4.3 and 4.4), in which the as yet undescribed *Serrodiscus daedalus* Öpik, 1975 was referred to as Undescribed Genus 2. Revision of *Serrodiscus* will require consideration of a much fuller range of the 19 species currently referred to the genus than has been possible here. Secondly, cladistic analysis suggests that *Opsidiscus* and *Helepagetia* should be regarded as synonyms. However, recognition of either of these genera may render *Pagetia* paraphyletic. The phylogeny of this group is therefore in need of further investigation, based on a wider range of taxa. Finally, *Mallagnostus* was found to be a paraphyletic assemblage with respect to *Tannudiscus*, *Chelediscus*, *Jinghediscus* and agnostids. However, Jell's synonymy of *Ladadiscus* Pokrovskaya, 1959 with *Mallagnostus* Howell, 1935 is supported based on the close relationship between the type species *L. limbatus* Pokrovskaya, 1959 (p. 168, pl. 11, figs 5-8, 10-15, 17) and *Agnostus desideratus* (Walcott, 1890, p. 39). Again, the other species referred to this genus, *Mallagnostus bonus* (Egorova *in* Egorova *et al.*, 1987, p. 52, pl. 1, fig. 8), *M. granulatus* (Soloviev, 1964, p. 37, pl. 1, fig. 1, text-fig. 1) and *M. semaensis* (Romanenko *in* Repina and Romanenko, 1978, p. 112, pl. 3, figs 4-5, 7), need to be considered before the genus can be adequately revised.

5. CONCLUSIONS AND SUGGESTIONS FOR FURTHER WORK

IT is now widely accepted amongst trilobite workers that an adequate classification must be based on phylogenetic relationships (Adrain and Westrop 1999). Only eight previous phylogenetic studies of Cambrian taxa based on modern cladistic methods have been published (Hughes and Ruston 1990; Babcock 1994; Westrop *et al.* 1996; Sundberg and McCollum 1997; Lieberman 1998, 1999*b*, 2001; Sundberg 1999). In total these papers include analyses of 16 cladistic character distribution matrices. The majority of these have been of very limited scope in terms of the number of taxa and characters considered. Only four have included more than 20 terminals (analyses of the Oryctocephalinae by Sundberg and McCollum [22 terminals], the Ptychagnostidae by Westrop *et al.* [44], the Olenelloidea [26] and Olenellina [26] by Lieberman 1998 and 2001, respectively). Against this background, the two studies presented here concerned solely with trilobites, including 49 and 83 taxa, represent a very significant contribution to knowledge of Cambrian trilobite phylogeny.

The Ptychopariina includes a large proportion of Cambrian trilobite diversity and is probably ancestral to most groups of post-Cambrian trilobites. Resolution of the phylogenetic relationships within the group is therefore crucial to a better understanding of the initial radiation of trilobites as a whole. The taxonomy of the group has been less stable even than that of other Cambrian trilobites (Fortey 1990*b*, 2001; Sundberg 1999). It has been suggested that this reflects pervasive iteration, and consequent difficulty in identifying evolutionary lineages, within the group. This has lead to suggestions that cladistic methods are inadequate for resolving ptychoparioid phylogeny and that hypotheses about ptychoparioid relationships must instead rely on a combination of stratigraphic data and overall similarity (Sundberg 1994, Palmer 1965).

The analysis of the phylogeny of the 'conocoryphids' in Part Two represents only the second cladistic study of the ptychoparioids. Whilst the 'conocoryphids' themselves are a small part of the group, they are morphologically generalized and hence typical of the ptychoparioid problem as a whole (Rasetti 1951, 1972; Schwimmer 1975; Fortey 1990*b*).

Along with Sundberg's (1999) study of the Alokistocaridae, another generalized family, this work demonstrates the potential for cladistic methods to resolve ptychoparioid phylogeny. These studies provide no evidence that levels of homoplasy are unusually high in the Ptychopariida (*contra* Sundberg 1994). In contrast, comparison of the disparity of the blind ptychoparioid clades identified above with that of the original polyphyletic 'Conocoryphidae' suggests that ptychoparioid clades form morphologically discrete groups. Whilst it is undeniable that discoveries of new material of described taxa will aid the resolution of the ptychoparioid problem (see e.g. the preliminary results based on new discoveries of marjumioid ontogenies shown in Hughes *et al.* 1999), there is clearly considerable scope for cladistic analysis of detailed morphological features to clarify relationships on the basis of existing material.

Intriguingly, in contrast to suggestions that phylogenetic analysis is made difficult by the generalized morphology of many ptychoparidoid taxa, existing analyses may suggest that ptychoparioids are rather character rich relative to other trilobite groups. On average, the two matrices that have dealt with members of the Ptychopariina (Sundberg 1999 and Part Two, herein) have included 2.3 characters per taxon, whereas the 10 analyses of various groups within the Olenellina (Lieberman 1998, 1999*b*, 2001) have only employed 1.7 characters per taxon and the three analyses of Agnostida (Babcock 1994; Westrop *et al.* 1996 and Part Four, herein) 1.2 characters per taxon. These difference are particularly surprising considering that both analyses of ptychoparioids deal with species-level relationships within 'generalized' families and many studies of other groups have dealt with higher-level relationships. Of course, these differences may just as well reflect differences in character construction and coding between workers than genuine differences in morphological variability.

The whole of the Ptychopariina clearly remains in need of phylogenetic attention. Whilst this is a daunting task given the size of the taxon, there is no reason to suppose any methodological barriers prevent relationships within the group from being resolved. As Fortey (1990*b*) has suggested, one possible approach would be to conduct a broad analysis of well known taxa from throughout the group, including representatives of probable descendant

clades (Asaphida, Proetida, Phacopida, Harpina, and Olenina), in order to identify synapomorphies defining well supported clades. This could form the basis for more detailed study of sub-groups. For example, the families Catillicephalidae (or at least some members of it, if it proves polyphyletic, see Fortey 1983, Fortey and Chatterton 1988), Lonchocephalidae and Onchonotopsidae share an unusually straight and strongly angled facial suture that may be synapomorphic (Rasetti 1954), and the families Menomoniidae, Nepeiidae and Norwoodiidae are also likely to form a clade (Öpik 1967).

With the exception of Lieberman's study of the Olenellina (1998, 1999*b*, 2001), the analysis of the phylogeny of the Agnostida presented in Part Four of this work represents the most substantial cladistic analysis of any trilobite group. Lieberman's study consisted of an analysis of the phylogeny of the Olenelloidea at the generic level (1998), followed by analyses of the phylogeny of subfamilies and genera separately (1999) and confirmation of the monophyly of the Olenelloidea (2001). In combining a thorough sample of taxa with a broad taxonomic scope, the analysis presented here goes further than Lieberman's study (see Fortey 2001 on the limitations of Lieberman's approach) in demonstrating the utility of cladistic methods for understanding the phylogeny of major trilobite groups.

The results presented here strongly confirm that the agnostids are trilobites closely related to eodiscinids (e.g. Jell 1975, Fortey 1990*b*, Fortey and Theron 1994) and constitute strong evidence against the view that agnostids are more closely related to crustaceans than to eodiscinids and other trilobites (e.g. Walossek and Müller 1990; Shergold 1991; Bergström 1992). The paraphyly of the eodiscinids with respect to the agnostids, and division of more derived Agnostida into two large clades (recognised as an emended Agnostina and Eodiscina) are also strongly supported.

If the paraphyly of the Eodiscina with respect to the Agnostina represents a common pattern amongst high-level trilobite taxa, claims that much of the early history of cladogenesis in trilobites is not recorded in known fossils (Briggs and Fortey 1992; Fortey *et al.* 1997) should be treated with caution. In contrast, the general phylogenetic relationships between the main trilobite groups originating in the Early Cambrian are fairly clear (Fortey 2001) and there

is little reason to suppose that key taxa are unknown. The Fallotaspidoidea are likely to be paraphyletic with respect to the Redlichiina or to the Redlichiina and Olenellina (Lieberman 1998, 2001), depending on whether they or olenellids are the basal trilobite group. The Agnostida are likely to have evolved by heterochrony from the Redlichiida (e.g. Fortey 1990*b*, Jell 1975, 1997). No systematic comparison of the morphology of larval redlichiids and adult eodiscinids has been made, but the absence of major morphological differences is illustrated by the assignment of probable juvenile redlichioids, such as *Dipharus clarki* Korobov 1980 to the Eodiscina (Jell, 1997, p. 384). The Redlichiida are likely to be paraphyletic with respect to the Corynexochida, Lichida and Ptychopariina, via taxa currently assigned to the Ellipsocephaloidea and Paradoxidoidea (Geyer 1990). The Ptychopariina are likely to be polyphyletic with respect to remaining Cambrian Orders and Suborders (see Figure 2.1 herein).

The analysis of the Agnostida in Part Four has clearly failed to resolve many aspects of the phylogeny of the group. Relationships within the paraphyletic basal group here included in the paraphyletic 'Calodiscina' are in particular need of attention. Both further analysis, to confirm the degree of resolution possible with the data presented here, and additional primary systematic work are necessary before the phylogeny of the group is fully understood.

It seems likely that much of the variation in results between analytical conditions is due to the very large amount of missing data in the matrix. Selectively excluding poorly known taxa (especially many Russian species, e.g. those described by Korobov 1980) from the database may dramatically improve the robustness of the results. Considering the complexity of the analysis, there is also scope to allow more complete investigation of the matrix by collapsing well supported clades to single terminals (e.g. Lieberman 2001, p. 99), making analysis of relationships amongst remaining taxa more tractable. Finally, many of the members of Jell's (1997) Hebediscidae are poorly preserved and inadequately described. Re-collecting at the type localities of these taxa, and re-describing existing specimens should add considerably to our understanding of the early evolution of the Agnostida.

It is clear, from both cladistic analysis and comparison of agnostid and eodiscinid morphology, that the morphological distinctiveness of the agnostids has been considerably

overstated. Many features of their supposedly distinctive body-plan evolved before the origin of the group, amongst the weymouthiid eodiscinids. Preliminary comparison of branch lengths suggests that no unusual levels of morphological innovation were involved in the origin of the agnostids compared to other lineages of Agnostida. Further investigation of such patterns will require a much more robust estimate of phylogeny (see e.g. Wagner 1995, 1997).

In contrast to the situation in trilobites, the relationships of arthropods known only from Cambrian and later Lagerstätten such as the Burgess Shale, have received considerable attention. However, results from previous studies have been highly contradictory (Figures 3.2, 3.3) and have generally not identified well-supported clades. The hypothesis of the relationships between arachnomorph arthropods presented in Part Two is superior to previous cladistic studies in providing detailed discussion of primary hypotheses of homology and by including a much more complete range of terminal taxa. Perhaps most importantly, this analysis provides, for the first time, convincing synapomorphies for the Arachnomorpha and for major clades within the group.

Taxa included here in the Arachnomorpha were central to Gould's (1989) original argument that Burgess Shale arthropods represented a range of entirely extinct body-plans. Head segmentation has received considerable attention as a feature that is remarkably conservative amongst extant arthropod classes, but supposedly highly convergent in the Cambrian (e.g. Stürmer and Bergström 1978; Bruton and Whittington 1983; Delle Cave and Simonetta 1991). Far from supporting the 'grabbag of available arthropod characters' that Gould (1989, p. 215) envisaged, the analysis presented in Part Three suggests that patterns of head segmentation were remarkably conservative amongst arachnomorphs.

The phylogenetic hypotheses presented here represent a valuable resource for understanding morphological evolution in Cambrian arthropods, not only in terms of branching patterns but also as a direct source of morphological information. Studies of morphological evolution are increasingly based on discrete character data, as employed in cladistic analysis (e.g. Wills *et al.* 1994, Wagner 1997, Foote 1999). It has not been the intention to fully explore the implications of the phylogenetic hypotheses presented here for understanding arthropod

evolution during the Cambrian. Instead, the morphological investigations in each part of this work are indicative of the importance of phylogeny for understanding morphological evolution. Unbiased assessments of morphological diversity (disparity), the evolution of particular characters or character complexes and rates of morphological evolution all require an explicit phylogenetic hypothesis.

Taken together, the phylogenetic hypotheses presented here suggest a radically different view of Cambrian evolution than that suggested by Gould (1989). Many Cambrian taxa, whether large groups such as agnostids or species based on a single specimen such as *Helmetia expansa*, do show distinctive features that defy obvious hypotheses of homology. For example, Briggs (1981, p. 38) once suggested of Burgess Shale arthropods that 'each species has unique characteristics, while those shared tend to be generalized and common to many arthropods. Relationships between these contemporaneous species are, therefore, far from obvious, and possible ancestral forms are unknown'. This has been taken as evidence that morphologically similar taxa either never existed or were not preserved – leading to suggestions of unusually rapid morphological evolution or a highly incomplete fossil record. When placed in their correct phylogenetic context, the origins of these features becomes clear and they can be seen as relatively minor variations on the ancestral condition – no unusual evolutionary process seems necessary to account for the evolution of the great appendages of *Leanchoilia* from those of *Jianfengia,* or for the evolution of the agnostid cephalic axis from that of *Chelediscus* or *Tannudiscus.*

Alternatively, some diverse Cambrian taxa, such as ptychopariid or olenellid trilobites, seem to show a bewildering variety of minor variations within a similar basic structure. This leads to suggestions of morphological constraint and iterative evolution. The strength of a hierarchical pattern of morphological variation can only be assessed by phylogenetic analysis. Neither previous studies (Lieberman 1998) nor the present work (see Part Two) support suggestions that levels of homoplasy were unusually high in Cambrian trilobites.

Patterns of morphological evolution can only be understood in a phylogenetic context. The analyses presented here have demonstrated that the careful application of cladistic

methods can resolve the major issues in Cambrian trilobite phylogeny. These analyses provide no support for suggestions of unusual patterns of morphological evolution. When their phylogeny is better known, Cambrian trilobites and other arachnomorphs should play a central role in finally understanding what, if anything, was unusual about evolution in the Cambrian.

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INSTITUTIONAL ABBREVIATIONS

BMNH, Department of Palaeontology, The Natural History Museum, London, UK.,

BUGM, Department of Earth Sciences, University of Bristol, UK.

CSGM, Central Siberian Geological Museum, Novosibirsk, Russia.

GIN, Museum of the Geological Institute, Russian Academy of Sciences, Moscow, Russia.

ICS, Institute for Cambrian Studies, Boulder, Colorado, USA.

MMG, Museum of the Ministry of Geology, Tashkent, Uzbekistan.

MPZ, Museum of Palaeontology, University of Zaragoza, Spain.

NMW, National Museum of Wales, Geology Department, Cardiff, UK.

ROM, Department of Invertebrate Paleontology, Royal Ontario Museum, Toronto, Canada.

SM, Sedgwick Museum, University of Cambridge, UK.

SMF, Senckenberg Museum, Frankfurt, Germany.

USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

APPENDICES

Appendix 1. Characters and character states used in analyses of "conocoryphid" phylogeny in Part 2. Character state distributions are shown in Table 2. Some characters are discussed further in the text. The three sets of characters used to investigate the effects of alternative assumptions on the results of phylogenetic analyse were: (1) quantitative characters, numbers 1, 18, 19, 22, 23, 24, 26, 27, 39, 56, 59, 63, 72, 73, 79, 82, 83, 84 and 85; (2) effacement characters, 8, 9, 30, 32 and 54, and; (3) other characters, 43 and 48. The conditions for characters to be coded as 'not applicable' (see text) are shown in square brackets after the character description. For example, character 2 could only be coded for taxa with a backwardly convex anterior border, coded as state 2 of character 1 (1:2), and is coded as 'not applicable' for taxa with other states of character 1.

1. Adaxial expansion (sag.) of anterior cephalic border. 0: border of even width or border expands gradually without change in the curvature of the border furrow, 1: border expands such that posterior edge of border becomes truncated in front of the glabella, 2: border expands such that a transverse line cuts the posterior edge of the border in more than two places.
2. Degree of backward convexity of the anterior cephalic border, in dorsal view [1: 2]. 0: border weakly convex, 1: border strongly convex.
3. Anterior cephalic border constricted adaxially. 0: absent, 1: present.
4. Cephalic border furrow partially effaced in front of the glabella. 0: absent, 1: present.
5. Shape of the anterior cephalic border, in sagittal cross-section. 0: convex,1: flattened.
6. Degree of convexity of convex anterior cephalic borders, in sagittal cross-section [5: 0]. 0: strongly convex, 1: more weakly convex.
7. Slope of flattened anterior cephalic borders [5: 1]. 0: sloping downwards anteriorly, 1: sloping upwards anteriorly, 2: more or less horizontal.
8. Definition of the anterior cephalic border. 0: defined by strong border furrow, 1: defined by faint furrow and/or change in convexity, 2: border completely confluent with genae.
9. Effacement of the posterior cephalic border furrow on external surface. 0: not effaced, 1: posterior border faintly discernible, defined by a wide and shallow furrow or by a change in convexity, 2: effaced entirely or represented only by lack of sculpture on external surface.
10. Cephalic border furrow continuous across genal angles. 0: present, 1: absent, furrows become effaced at or near genal angles.
11. Posterior cephalic border furrow turns forwards before becoming effaced [10: 1]. 0: absent, effacement occurs well before genal angle, 1: present.
12. Posterior cephalic border furrow arches forwards well inside the genal angles [10: 0]. 0: absent, cephalic border furrow closely follows the posterolateral margin of the cephalon, 1: present.
13. Shape of the posterior cephalic border furrow. 0: furrow of approximately even width along entire length, 1: furrow gradually expands laterally, 2: furrow expands laterally then contracts, resulting in an ovate appearance.

14. Anterior margin of cephalon transverse axially. 0: absent, 1: present.

15. Shape of the anterolateral corners of cephalon. 0: evenly rounded, 1: angular.

16. Expansion of the lateral margins of cephalon. 0: absent, maximum cephalic width at posterior margin, 1: present, maximum cephalic width anterior to the posterior margin.

17. Anterior arch of the cephalon, in anterior view. 0: absent, 1: present.

18. Length of cephalon (sag.) as proportion of maximum width of cephalon (trans.). 0: shorter (0.35-0.45), 1: approximately half as long as wide (0.45-0.55), 2: slightly longer (0.55-0.65), 3: moderately longer (0.65-0.75), 4: much longer (>0.75).

19. Position of facial sutures on dorsal surface. 0: marginal or sutures absent, 1: sutures remain on cephalic border, 2: sutures reach border furrow but do not cross it, 3: sutures cross border furrow onto cheek.

20. Facial sutures sinuous. 0: absent, 1: present.

21. Position of facial sutures at the genal angles result in posteriorly projecting posterolateral corners of the cranidium. 0: absent, 1: present.

22. Length of glabella (sag., excluding occipital ring) as proportion of length of cephalon (sag.). 0: very short (<=0.49), 1: short (0.5-0.6), 2: long (0.61-0.71), 3: very long (>=0.72).

23. Width of glabella (trans.) at base as proportion of maximum width of cephalon (trans.). 0: very narrow (<=0.25), 1: narrow (0.251-0.34), 2: wide (0.341-0.43), 3: very wide (>=0.431).

24. Width of glabella (trans.) at base as proportion of length of glabella (sag., excluding occipital ring). 0: narrow (<=0.94), 1: medium (0.95-1.09), 2: wide (>=1.1).

25. Shape of glabella. 0: strongly tapers forward, 1: approximately parallel sided, 2: expands anteriorly.

26. Shape of anterior termination of glabella. 0: rounded,1: somewhat blunt, 2: square.

27. Number of visible pairs of lateral glabellar furrows. 0: 0, 1: 1, 2: 2, 3: 3, 4: 4.

28. Strength of posterior lateral glabellar furrows [27: 1-4]. 0: strongly defined, 1: weakly defined.

29. Lateral glabellar furrows defined by lack of sculpture only [27: 1-4]. 0: absent, 1: present.

30. Condition of the preglabellar furrow. 0: present, 1: less firmly incised than axial furrows, 2: completely effaced.

31. Glabella defined anteriorly by change in convexity from preglabellar field. 0: absent, 1: present.

32. Condition of axial furrows. 0: present, 1: effaced anteriorly, 2: entirely effaced.

33. Lateral glabellar furrows indicated on internal moulds by shallow rounded depressions. 0: absent, 1: present.

34. S1 furrows bifurcate adaxially on external surface. 0: absent, 1: present.

35. Shape of S1 furrows. 0: straight or simply curved, 1: recurved backwards and then inwards.

36. Length of S2 furrows. 0: short (shorter than sagittal length of L4), 1: longer.

37. Shape of S2 furrows. 0: transverse, 1: oblique backwards.

38. Length of S3 furrows. 0: pits or very short slits, 1: long and deep furrows.

39. Length of occipital ring (sag., from midpoint of SO) as a proportion of the length of the glabella (sag., excl. occipital ring). 0: short (<=0.2), 1: medium (0.21-0.37), 2: long (>=0.38).

40. Broad-based posteriorly directed occipital spine. 0: absent, 1: present.

41. Occipital node. 0: absent, 1: present.

42. Pair of pits along posterior edge of occipital furrow. 0: absent (e.g. Pl. 1, figs 1, 7), 1: present (e.g. Fig. 2.2A; Pl. 4, fig. 9).

43. Eye ridges. 0: absent, 1: present only on internal moulds, 2: present on external surface.

44. Form of eye ridges [43: 1-2]. 0: highly curved, 1: more or less straight.

45. Direction of eye ridges [43: 1-2]. 0: eye-ridges run backwards and outwards obliquely, 1: eye-ridges run transversely or anteriorly and transversely.

46. Eye ridges project anteriorly before turning backwards [43: 1-2]. 0: absent, 1: present.

47. Nature of insertion of eye ridges adaxially [43: 1-2]. 0: into glabella, interrupting axial furrows with prominent raised ridges, 1: into axial furrows, axial furrows not interrupted by eye ridges.

48. Caecal network present on anterior genae. 0: absent, 1: present only on internal moulds, 2: present on external surface.

49. Prominent (compared to caecal network) reticulate sculpture present on genae. 0: absent, 1: present.

50. Genal node, caused by thickened eye ridge just abaxial to anterior axial furrows [43: 1-2]. 0: absent, 1: present.

51. Anterior branch of eye ridge runs around front of glabella (parafrontal band) [43: 1-2]. 0: absent, 1: present.

52. Presence of anterior genal ridges, other than eye ridges. 0: absent, 1: present.

53. Elevation of preglabellar field [55: 1]. 0: confluent with cheeks, 1: depressed relative to cheeks, in anterior view, 2: raised to form preglabellar boss.

54. Preglabellar field crossed by furrow, other than border furrows [55:1]. 0: absent, 1: weak furrows present, 2: clear furrows present.

55. Preglabellar field. 0: absent, 1: present.

56. Length of preglabellar field (sag.) as proportion of length of preglabellar area (sag.) [55: 1]. 0: very narrow (<= 0.3), 1: narrow (0.31-0.45), 2: approximately equal (0.46-0.6), 3: wide (0.61-0.75), 4: very wide (>= 0.76).

57. Nature of preglabellar boss [53: 2]. 0: confluent with anterior border, 1. separated from border by border furrow.

58. Tuberculate or spinose sculpture on cephalon. 0: absent, 1: present.

59. Density of tubercles [58: 1]. 0: sparse, 1: medium, 2: dense.

60. Pustulose sculpture on cephalon. 0: absent, 1: present.

61. Punctate sculpture on cephalon. 0: absent, 1: present.

62. Convexity of genae. 0: downsloping laterally (maximum height of genae at axial furrows), 1: independently convex (maximum height of genae abaxial to axial furrows).

63. Degree of genal convexity [62: 1]. 0: weakly convex, 1: elevated more or less to the level of glabella, 2: elevated clearly above the level of the glabella.

64. Genal spines. 0: absent, 1: present.

65. Angle of insertion of genal spines [64: 1]. 0: Genal spines directed backwards approximately parallel to the axis, 1: Genal spines directed obliquely outwards and backwards.

66. Length of genal spines as proportion of length of cephalon [64: 1]. 0: short (<= 0.45), 1: medium (0.46-0.65), 2: long (>= 0.65).

67. Genal spines gently sinuous in shape [64: 1]. 0: absent, 1: present.

68. Paradoublural line. 0: absent, 1: present.

69. Shape of paradoublural line [68: 1]. 0: extends evenly beyond border, 1: extends posteromedially to form plectrum.

70. Hypostomal condition. 0: conterminant, 1: natant.

71. Shape of hypostome (see Fortey, 1990). 0: primitive shape, 1: fused to rostral plate, 2: generalized ptychoparioid form.

72. Length of cephalon (sag.) as a proportion of length of entire exoskeleton (sag.). 0: cephalon proportionately small (<=0.3), 1: cephalon of intermediate proportional size (0.31-0.4), 2: cephalon proportionately large (>=0.41).

73. Number of thoracic segments. 0: less than 8, 1: 8, 2:13, 3: 14, 4: 15, 5: 17, 6: 18, 7: 20 or greater,

74. Nature of thoracic pleural terminations. 0: blunt, faceted terminations, 1: oblique falcate points, 2: extended to form spines.

75. Length of thoracic pleural spines [74: 2]. 0: short, 1: long.

76. Width of thoracic pleural furrows (exsag.). 0: wide (approx. half sag. pleural length or greater), 1: narrow (less than half pleural length). Note: pleural furrow width is very difficult to measure, because the boundaries of the furrows are often indistinct. This character was therefore coded conservatively, and the two states used are highly distinct in the taxa under consideration.

77. Direction of thoracic pleural furrows. 0: transverse, 1: oblique.

78. Shape of thoracic pleural furrows. 0: straight, 1: highly curved.

79. Width of thoracic axis (trans.) compared to width of whole segment (trans., excluding pleural spines) on anterior segments. 0: narrow (<=0.25), 1: medium (0.26-0.33), 2: wide (0.34-0.43), 3: very wide (>=0.44).

80. Macropleural spines on thoracic segments. 0: absent, 1: present.

81. Nature of pleural geniculations. 0: smoothly rounded, 1: prominently raised, with tubercles.

82. Length of pygidium (sag.) as a proportion of length of entire exoskeleton (sag.) 0: pygidium proportionately small (<=0.05), 1: pygidium of intermediate proportional size (0.06-0.1), 2: pygidium proportionately large (>=0.11).

83. Length of pygidial post-axial field. 0: post-axial field absent, 1: short (approx. equal to border width) post-axial field, 2: longer.

84. Width of pygidial axis (trans., anteriorly) as proportion of maximum width of pygidium (trans.). 0: axis narrow (<= 0.34), 1: axis of intermediate relative width (0.35-0.49), 2: axis broad (>-0.5).

85. Number of segments (excluding terminal piece) in pygidial axis. 0: 2, 1: 3, 2: 4, 3: 5, 4: 6.

86. Interpleural furrows on pygidium. 0: absent, 1: present.

87. Furrows on postaxial field of pygidium. 0: absent, 1: present.

88. Form of pygidial pleural furrows. 0: highly curved and very oblique backwards, 1: much less curved and run more directly transversely.

89. Anterior border constricted due to encroachment of the glabella. 0: absent, 1: present.

90. S1 lateral glabellar furrows transglabellar. 0: absent, 1: present.

91. Presence of palpebral lobes on genae. 0: absent, 1: present.

93. Palpebral lobes wider (trans.) than and elevated above eye ridges. 0: absent, 1: present.

93. Eye ridges divided from palpebral lobes. 0: absent, 1: present.

94. Width (sag.) of eye ridges. 0: thread-like, 1: wider.

95. Thoracic axial furrows zig-zag in shape. 0: absent, 1: present.

96. Pygidial border zonate. 0: absent, 1: present.

97. Broad form of pygidium. 0: semicircular fused plate, 1: tiny pauci-segmented elongate or circular plate.

Appendix 2. Synapomorphy scheme for ingroup nodes of the cladogram shown in Figure 2.4. Character numbers, reconstructed changes, number of steps and character consistency indices are shown for each apomorphy. Characters and character states numbered as in the previous section and Table 2.

Node 1. 20: 1>0 (1,0.167), 22: 3>2 (1,0.273), 75: 0>1 (1,0.200), 84: 2>1 (1,0.286), 85: 0>1 (1,0.444), 93: 0>1 (1,1.000), 94: 1>0 (1,1.000).

Node 2 (Atopidae). 19: 3>1 (2,0.158), 45: 0>1 (1,0.250), 46: 0>1 (1,1.000), 48: 0>2 (1,0.286), 49: 0>1 (1,0.250), 55: 1>0 (1,0.250), 62: 0>1 (1,0.250), 80: 0>1 (1,0.333), 91: 1>0 (1,0.200), 92: 1>0 (1,0.250).

Node 3. 5: 1>0 (1,0.333), 14: 0>1 (1,0.200), 22: 2>3 (1,0.273).

Node 4 (*Atops*). 6: 0>1 (1,0.111), 13: 0>1 (1,0.200), 60: 0>1 (1,0.091).

Node 5. 22: 2>1 (1,0.273), 24: 0>1 (1,0.167), 25: 1>0 (1,0.667), 28: 0>1 (1,0.125), 38: 1>0 (1,1.000), 47: 0>1 (1,1.000), 66: 2>0 (1,0.222), 77: 0>1 (1,0.333), 83: 0>1 (1,0.667), 84: 1>0 (1,0.286).

Node 6. 2: 0>1 (1,1.000), 5: 1>0 (1,0.333), 20: 0>1 (1,0.167), 39: 1>0 (1,0.400), 51: 1>0 (1,0.500), 69: 0>1 (1,0.500), 73: 5>2 (3,0.538), 82: 1>2 (1,0.400), 85: 1>2 (1,0.444).

Node 7. 48: 0>2 (1,0.286), 74: 2>1 (1,0.667), 85: 2>3 (1,0.444), 88: 0>1 (1,0.500).

Node 8. 13: 0>2 (1,0.200), 39: 0>1 (1,0.400), 42: 0>1 (1,0.250), 60: 0>1 (1,0.091), 66: 0>1 (1,0.222), 73: 2>3 (1,0.538), 77: 1>0 (1,0.333), 86: 1>0 (1,0.500).

Node 9 (Conocoryphidae). 17: 0>1 (1,0.500), 19: 3>2 (1,0.158), 20: 1>0 (1,0.167), 27: 4>3 (1,0.250), 43: 2>1 (1,0.200), 48: 2>1 (1,0.286), 50: 0>1 (1,0.333), 53: 0>1 (1,0.333), 58: 0>1 (1,0.111), 62: 0>1 (1,0.250), 85: 3>2 (1,0.444), 91: 1>0 (1,0.200), 92: 1>0 (1,0.250).,

Node 10 (*Bailiaspis*). 1: 0>2 (2,0.200), 13: 2>0 (1,0.200), 14: 0>1 (1,0.200), 18: 1>2 (1,0.190), 20, 0>1 (1,0.167), 28: 1>0 (1,0.125), 50: 1>0 (1,0.333), 56: 2>1 (1,0.308).

Node 11. 5: 0>1 (1,0.111), 15: 0>1 (1,0.500), 18: 2>1 (1,0.190), 19: 2>1 (1,0.158), 20: 1>0 (1,0.167), 25: 0>1 (1,0.167), 44: 0>1 (1,0.250), 45: 0>1 (1,0.250).

Node 12 (*Tchaiaspis*) . 23: 1>0 (1,0.231), 24: 1>0 (1,0.167), 36: 1>0 (1,0.333), 53: 0>2 (2,0.333), 58: 0>1 (1,0.333).,

Node 13. 3: 0>1 (1,0.500), 13: 2>0 (1,0.200), 19: 2>1 (1,0.158), 26: 0>1 (1,0.167), 28: 1>0 (1,0.125), 53: 1>2 (1,0.333), 54: 0>2 (1,0.333), 56: 2>3 (1,0.308), 59: 2>1 (1,0.250), 63: 0>1 (1,0.333), 66: 1>2 (1,0.222), 82: 2>1 (1,0.400).

Node 14. 26: 1>2 (1,0.167), 59: 1>2 (1,0.250), 63: 1>2 (1,0.333).,

Node 15. 6: 0>1 (1,0.111), 18: 1> (1,0.190), 43: 1>0 (1,0.200).

Node 16. 21: 0>1 (1,1.000), 24: 1>2 (1,0.167).

Node 17. 13: 0>2 (1,0.200), 52: 0>1 (1,1.000), 56: 3>4 (1,0.308), 73: 3>4 (1,0.538).

Node 18 (*Elyx*). 3: 1>0 (1,0.500), 4: 0>1 (1,0.250), 14: 0>1 (1,0.200), 44: 0>1 (1,0.250), 50: 1>0 (1,0.333), 57: 1>0 (1,1.000).

Node 19. 22: 1>3 (2,0.273), 25: 0>2 (1,0.667), 27: 4>2 (2,0.250), 55: 1>0 (1,0.250), 70: 1>0 (1,0.500), 71: 2>1 (1,1.000), 73: 2>0 (2,0.538), 76: 0>1 (1,0.333), 79: 1>2 (1,0.429), 96: 0>1 (1,0.500).

Node 20 (Acontheinae). 5: 0>1 (1,0.333), 18: 1>3 (2,0.190), 20: 1>0 (1,0.167), 24: 1>0 (1,0.167), 27: 2>1 (1,0.250), 36: 1>0 (1,0.333), 72: 1>2 (1,0.667), 74: 2>0 (1,0.667), 89: 0>1 (1,0.500), 95: 0>1 (1,0.500).

Node 21. 18: 3>4 (1,0.190), 19: 3>0 (3,0.158), 23: 1>0 (1,0.231), 30: 0>2 (1,0.667), 41: 1>0 (1,0.143), 43: 2>0 (1,0.200), 61: 0>1 (1,0.333), 64: 1>0 (1,0.500), 65: 0>1 (1,0.250), 83: 1>0 (1,0.667), 91: 1>0 (1,0.200), 92: 1>0 (1,0.250).

Node 22 (Hartshillini). 8: 0>2 (1,0.333), 9: 0>2 (1,0.500), 10: 0>1 (1,0.333), 27: 1>0 (1,0.250), 31: 1>0 (1,1.000), 32: 0>2 (1,0.500), 73: 0>1 (1,0.538), 78: 0>1 (1,1.000), 84: 0>1 (1,0.286), 85: 2>0 (2,0.444).

Node 23 (*Hartshillia*). 40: 0>1 (1,0.500), 88: 0>1 (1,0.500), 95: 1>0 (1,0.500), 96: 1>0 (1,0.500).

Node 24. 1: 0>2 (2,0.200), 8: 0>1 (1,0.333), 9: 0>1 (1,0.500), 12: 0>1 (1,0.500), 13: 0>1 (1,0.200), 18: 1>2 (1,0.190), 30: 0>1 (1,0.667), 33: 0>1 (1,0.333), 37: 1>0 (1,1.000), 44: 0>1 (1,0.250), 65: 0>1 (1,0.250), 82: 1>0 (1,0.400), 83: 1>2 (1,0.667), 87: 0>1 (1,1.000).

Node 25 (Holocephalidae). 11: 1>0 (1,0.500), 19: 3>1 (2,0.168), 27: 4>3 (1,0.250), 49: 0>1 (1,0.250), 73: 5>6 (1,0.333), 76: 0>1 (1,0.333), 91: 1>0 (1,0.200), 92: 1>0 (1,0.250).

Node 26. 7: 0>1 (1,1.00), 9: 1>0 (1,0.500), 13: 1>0 (1,0.200), 18: 2>1 (1,0.190), 22: 1>0 (1,0.273), 23: 1>0 (1,0.231), 28: 1>0 (1,0.125), 33: 1>0 (1,0.333), 42: 0>1 (1,0.250), 48: 0>2 (1,0.286), 53: 0>1 (1,0.333), 56: 2>3 (1,0.308), 81: 0>1 (1,1.000).,

Node 27 (*Dasometopus*). 1: 2>0 (2,0.200), 12: 1>0 (1,0.500), 34: 0>1 (1,1.000), 39: 1>2 (1,0.400), 56: 3>4 (1,0.308), 58: 0>1 (1,0.111), 80: 0>1 (1,0.333), 84: 0>1 (1,0.286), 85: 1>0 (1,0.444).

Node 28. 18: 1>0 (1,0.190), 59: 2>0 (2,0.250), 60: 0>1 (1,0.091), 68: 0>1 (1,0.333).

Node 29 (*Meneviella*). 8: 1>0 (1,0.333), 72: 1>0 (1,0.667), 73: 6>7 (1,0.538).

Node 30. 26: 0>1 (1,0.167), 29: 0>1 (1,0.333), 32: 0>1 (1,0.500), 39: 1>0 (1,0.400), 41: 1>0 (1,0.143), 43: 2>0 (1,0.200), 67: 0>1 (1,0.500), 75: 1>0 (1,0.200).

Node 31. 8: 1>2 (1,0.333), 10: 0>1 (1,0.333), 18: 2>3 (1,0.190), 23: 1>2 (1,0.231), 61: 0>1 (1,0.333), 79: 1>0 (1,0.429).

Node 32. 13: 1>0 (1,0.200), 24: 1>0 (1,0.167), 27: 3>0 (3,0.250), 32: 1>0 (1,0.500), 33: 1>0 (1,0.333), 66: 0>2 (1,0.222).

Appendix 3. Intertaxon near-euclidean distance matrix for 'conocoryphid' taxa

Calculated following the method of Wills *et al.* (1993). Values are in units of character state difference.

		1	2	3	4	5	6	7	8	9	10	11
1	*Atopina antiqua*	-										
2	*Atops rupertensis*	3.254	-									
3	*A. trilineatus*	2.146	2.074	-								
4	*Bailiaspis bobrovi*	5.137	4.432	4.037	-							
5	*B. dalmani*	4.703	5.325	4.762	2.717	-						
6	*B. glabrata*	5.492	5.815	5.092	3.175	3.238	-					
7	*B. venusta*	4.194	4.084	3.861	3.154	2.321	3.278	-				
8	*Bailiella aequalis*	4.21	4.757	4.336	3.508	3.007	3.249	3.232	-			
9	*B. baileyi*	4.86	5.196	4.599	3.642	3.025	2.719	2.232	2.647	-		
10	*B. emarginata*	4.3	4.797	3.978	3.683	2.959	2.56	2.393	2.431	1.114	-	
11	*B. lantenoisi*	5.522	5.606	4.811	3.801	3.622	2.821	3.417	2.844	1.96	2.373	-
12	*B. levyi*	4.921	5.422	4.919	4.128	3.569	1.768	3.185	2.562	2.425	2.564	2.384
13	*Conocoryphe caecigena*	4.597	4.964	4.524	3.67	3.718	3.096	3.603	2.554	2.772	2.377	2.565
14	*C. sulzeri*	4.813	5.677	5.057	3.603	2.998	3.304	3.491	2.687	2.205	2.01	3.036
15	*Cornucoryphe schirmi*	5.236	5.132	4.747	3.785	3.481	2.846	3.616	3.271	2.983	2.845	2.11
16	*Couloumania heberti*	4.642	5.018	4.827	3.797	3.202	3.642	3.127	2.117	2.382	2.29	2.888
17	*Ctenocephalus (C.) bergeroni*	5.445	4.392	4.223	4.671	4.792	4.586	3.827	3.832	3.314	3.894	3.9
18	*C. (C.) coronatus*	6.081	5.392	5.08	4.854	4.824	4.335	4.702	4.066	3.837	4.184	4.157
19	*C. (Hartella) antiquus*	4.92	4.657	4.452	4.194	4.197	3.809	4.001	3.396	3.498	3.969	3.848
20	*C. (H.) exsulans*	5.283	4.84	4.417	3.714	3.92	3.695	4.283	3.727	3.351	3.487	3.586
21	*C. (H.) matthewi*	5.856	5.233	5.09	4.055	4.045	3.627	4.424	3.208	3.38	3.829	3.779
22	*C. (H.) terranovicus*	4.371	4.394	3.906	3.49	3.438	3.712	3.675	2.954	3.326	3.673	3.489
23	*Dasometopus breviceps*	5.981	5.788	5.808	5.409	5.417	5.219	5.251	5.091	5.388	4.558	5.558
24	*D. granulatus*	4.726	4.414	4.379	4.062	4.784	4.374	3.986	4.257	4.38	3.86	4.976
25	*D. maensis*	5.981	5.723	5.852	5.303	5.216	5.201	5.049	5.344	5.775	4.831	5.81
26	*Elyx laticeps*	5.419	5.129	4.652	3.571	3.908	4.589	3.953	3.974	3.779	3.931	3.804
27	*E. matthewi*	4.69	4.647	4.473	3.779	3.502	4.187	3.225	3.388	3.535	3.205	3.578
28	*Hartshillia clivosa*	4.766	7.34	5.986	7.948	7.688	6.404	7.209	7.134	6.516	7.117	6.768
29	*H. inflata*	4.766	7.424	6.324	7.948	7.688	6.404	7.075	7.042	6.906	7.027	6.237
30	*Hartshillina spinata*	4.766	7.295	6.047	7.336	7.366	6.182	7.307	6.666	7.318	6.948	6.994
31	*Holocephalina leve*	6.791	6.633	6.131	6.117	6.012	4.806	5.684	5.549	5.257	5.45	4.867
32	*H. primordialis*	7.028	6.406	5.827	5.482	5.209	4.736	5.36	5.236	4.892	5.254	4.865
33	*Holocephalites incertus*	5.07	6.635	5.448	6.371	5.97	5.191	6.076	5.55	5.764	6.18	5.502
34	*Meneviella venulosa*	5.91	5.937	5.872	3.89	4.298	4.38	4.851	4.996	5.071	4.832	5.813
35	*M. viatrix*	5.189	5.516	5.738	4.569	4.625	4.435	5.107	4.675	4.897	4.648	5.592
36	*Parabailiella languedocensis*	3.885	4.426	4.049	3.513	2.939	3.308	2.369	2.132	1.749	1.666	2.755
37	*Pseudatops reticulatus*	3.434	3.109	2.389	4.924	5.337	5.203	4.799	4.695	4.505	4.626	4.878
38	*Sdzuyella stremina*	4.326	5.963	4.671	5.783	5.635	4.573	5.145	5.537	5.001	5.171	4.955
39	*Tchaiaspis sdzuyi*	6.135	4.98	5.064	2.708	4.247	4.572	4.317	4.591	4.748	4.66	4.808
40	*Tchaiaspis sp. nov.*	5.512	4.644	4.804	2.647	3.748	3.786	3.782	4.064	4.467	4.276	4.705

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15	2.711	2.963	3.259	-											
16	3.278	2.748	1.745	3.3	-										
17	4.486	3.922	3.295	4.114	3.196	-									
18	4.312	4.183	3.791	4.123	3.559	0.712	-								
19	4.199	3.8	2.987	3.789	2.763	1.624	1.797	-							
20	4.293	3.327	3.225	3.393	2.902	2.223	2.219	1.676	-						
21	4.285	4.009	3.114	3.575	2.978	2.181	2.69	1.443	2.321	-					
22	4.139	3.616	2.796	3.227	2.958	2.199	2.416	1.449	1.75	1.539	-				
23	5.485	5.165	5.706	5.513	5.521	5.232	5.336	5.045	4.588	4.942	4.99	-			
24	4.583	4.171	4.815	4.687	4.324	4.889	5.024	4.563	4.304	4.394	4.114	1.855	-		
25	5.92	5.513	6.072	5.553	6.037	5.661	5.688	5.143	4.37	5.077	4.87	1.422	2.319	-	
26	4.327	4.439	3.965	3.735	3.935	4.295	4.429	4.179	3.908	4.034	3.182	4.675	4.802	4.949	-
27	4.015	4.026	3.414	3.267	3.342	3.457	3.665	2.816	2.523	2.987	2.235	4.648	4.334	4.421	2.846
28	6.541	6.649	6.922	6.768	6.826	7.317	7.277	6.554	6.881	7.192	6.375	7.656	6.573	7.474	7.563
29	6.564	6.464	6.859	6.979	6.413	7.098	7.108	6.344	6.881	7.192	6.375	7.705	7.016	7.64	7.468
30	7.378	6.249	7.515	7.519	7.325	7.161	7.706	6.128	6.222	6.555	5.869	7.023	6.593	7.477	7.341
31	5.248	4.882	5.908	4.99	5.749	6.483	6.164	6.161	5.946	5.988	5.291	6.218	5.566	6.252	6.221
32	4.883	5.017	5.45	4.722	5.607	6.442	6.078	5.958	5.699	5.376	5.404	5.491	5.014	5.558	5.401
33	5.372	5.481	6.217	5.455	6.005	6.879	6.669	6.423	6.307	6.191	5.77	5.504	4.881	5.139	6.351
34	5.682	5.034	5.951	5.374	5.618	5.664	5.765	5.135	4.539	4.495	4.442	3.207	2.733	3.664	4.948
35	5.323	4.832	5.607	5.465	5.429	5.52	5.736	4.928	4.436	4.392	4.364	3.284	2.379	3.574	4.921
36	2.838	2.249	1.868	2.784	1.713	2.899	3.169	2.277	2.351	2.564	2.708	4.992	3.884	5.46	3.582
37	5.113	4.695	4.904	5.015	4.816	5.047	5.34	5.039	4.885	5.236	4.431	5.056	3.957	4.894	5.188
38	4.555	5.239	5.334	4.887	5.215	5.94	6.116	5.509	5.699	5.987	5.275	6.84	5.733	6.533	5.973
39	4.778	4.958	4.529	4.517	4.4	3.742	4.412	3.297	3.935	3.999	3.519	4.922	4.784	4.576	3.914
40	4.088	4.57	4.544	4.345	4.231	4.579	4.784	3.888	4.148	4.148	3.84	5.067	3.956	4.64	4.695

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29	6.952	1.457	-											
30	6.712	1.467	2.933	-										
31	6.142	4.95	4.738	5.624	-									
32	5.672	6.788	6.32	6.857	3.23	-								
33	6.357	4.239	4.525	5.361	3.939	4.578	-							
34	4.495	7.239	7.851	7.894	5.168	4.543	4.653	-						
35	4.133	6.871	7.742	7.855	5.216	4.819	5.003	2.491	-					
36	2.567	6.906	6.583	7.175	5.752	5.326	6.105	5.428	5.222	-				
37	5.012	6.155	6.201	5.77	5.457	5.555	4.933	4.963	4.354	4.323	-			
38	5.795	3.561	3.788	3.55	2.958	4.15	3.509	5.558	5.312	5.102	4.874	-		
39	3.341	8.33	8.33	7.407	6.998	6.145	6.305	4.36	4.52	4.05	5.752	6.528	-	
40	4.053	7.906	7.906	7.803	6.305	5.396	5.543	4.062	4.407	3.639	5.548	5.812	1.562	-

Appendix 4. Ordination of 'conocoryphid' taxa onto 40 PCO axes.

Derived from the matrix of near-euclidean distances shown above. Eigenvalues, percentages of the total variance expalined, and the cumulative total percentage are shown for each axis.

	1	2	3	4	5	6	7	8	9	10
Atopina antiqua	1.745	0.755	2.644	1.953	-0.424	-1.207	0.309	-0.238	-0.779	0.171
Atops rupertensis	-0.405	-0.149	2.862	1.881	0.328	1.790	0.079	0.089	0.368	-0.309
A. trilineatus	0.604	0.492	2.336	1.807	0.446	1.152	-0.283	0.243	0.310	0.088
Bailiaspis bobrovi	-1.771	-0.364	-0.008	1.120	1.707	-0.461	-0.545	-0.515	0.683	0.229
B. dalmani	-1.521	0.160	-0.764	1.120	0.605	-1.222	-0.540	-0.610	-0.614	-0.047
B. glabrata	-0.275	0.346	-1.681	0.064	0.381	-1.006	0.369	-0.288	1.096	-0.441
B. venusta	-1.140	0.481	-0.078	1.569	0.014	-0.350	-0.129	0.295	-0.221	-1.615
Bailiella aequalis	-1.032	0.814	-0.369	0.590	-0.502	-0.581	0.078	-0.411	0.341	1.097
B. baileyi	-0.986	1.220	-1.077	0.584	-0.785	0.030	0.144	-0.458	-0.334	-0.422
B. emarginata	-1.143	0.700	-0.565	0.967	-1.249	-0.608	-0.334	-0.136	0.507	-0.663
B. lantenoisi	-0.588	1.474	-1.549	0.228	-0.445	0.180	-0.522	0.864	0.434	0.467
B. levyi	-0.531	1.128	-1.578	0.984	-0.329	-0.370	0.829	0.854	0.235	-0.125
Conocoryphe caecigena	-0.401	0.887	-0.751	0.419	-0.797	-0.238	-0.036	-0.420	1.293	0.609
C. sulzeri	-1.270	1.803	-0.729	0.009	-0.503	-0.440	0.210	-0.329	-0.589	0.443
Cornucoryphe schirmi	-0.882	0.951	-1.324	0.370	-0.012	0.481	-0.243	0.779	-0.173	0.463
Couloumania heberti	-1.104	1.657	-0.369	0.017	-0.544	-0.219	0.589	-0.194	-0.510	0.363
Ctenocephalus (C.) bergeroni	-1.534	1.350	1.206	-1.585	-0.160	1.147	0.594	0.038	0.078	-0.497
C. (C.) coronatus	-1.470	1.182	0.341	-2.100	-0.337	1.381	0.867	0.245	-0.187	-0.190
C. (Hartella) antiquus	-0.957	1.085	0.999	-1.898	0.416	0.011	0.501	-0.187	0.034	-0.232
C. (H.) exsulans	-1.164	0.452	0.626	-1.729	-0.116	0.069	-0.300	-0.448	0.376	-0.047
C. (H.) matthewi	-1.375	0.440	0.065	-1.967	0.165	0.220	0.071	-0.899	0.035	0.525
C. (H.) terranovicus	-0.722	0.621	0.740	-1.257	0.550	0.207	-0.420	-0.564	-0.449	0.388
Dasometopus breviceps	-0.555	-3.194	0.509	-1.006	-1.817	-0.494	-0.365	0.788	0.571	-0.097
D. granulatus	-0.172	-2.398	0.648	0.236	-1.272	-0.246	0.594	-0.116	0.521	-0.279
D. maensis	-0.420	-3.489	0.631	-0.807	-1.031	-0.494	0.208	1.209	0.128	-0.335
D. laticeps	-1.395	-0.092	0.098	-0.137	0.217	0.025	-2.107	1.011	-1.177	0.437
E. matthewi	-1.331	0.174	0.647	-0.736	0.099	-0.530	-1.094	0.286	-1.013	-0.393
Hartshillia clivosa	5.432	0.794	0.419	-0.735	-0.184	-0.629	0.480	-0.164	-0.615	-0.305
H. inflata	5.251	1.498	0.103	-0.858	-0.264	-0.169	0.197	0.898	-0.404	-0.243
Hartshillina spinata	4.985	0.673	1.458	-1.334	0.833	-1.313	-1.242	-0.369	1.438	0.068
Holocephalina leve	2.859	-0.655	-2.598	-0.184	0.131	1.602	-0.399	-0.510	0.267	-0.386
H. primordialis	1.236	-1.496	-2.717	0.237	0.473	1.720	-0.872	0.060	0.075	-0.081
Holocephalites incertus	3.275	-1.778	-1.047	0.399	0.296	-0.147	1.226	0.954	-0.582	1.343
Meneviella venulosa	-0.438	-3.437	-0.634	-0.161	0.474	-0.114	0.290	-1.126	-0.667	-0.170
M. viatrix	-0.215	-3.074	-0.110	-0.093	-0.296	-0.171	0.305	-1.490	-0.753	0.045
Parabailiella languedocensis	-1.282	1.387	0.071	0.280	-0.597	-0.073	0.293	0.095	-0.135	-0.165
Pseudatops reticulatus	1.075	-0.704	1.725	1.403	-0.903	1.434	-0.159	-0.538	0.232	0.903
Sdzuyella stremina	3.400	0.432	-0.947	0.649	1.106	0.431	0.104	-0.374	-0.381	-0.701
Tchaiaspis sdzuyi	-2.148	-0.988	0.750	-0.741	2.279	-0.452	0.238	0.959	0.251	0.182
Tchaiaspis sp. nov.	-1.634	-1.136	0.013	0.436	2.047	-0.344	1.430	0.717	0.309	-0.081
Eigenvalues	155.8	83.753	60.960	46.331	27.746	24.690	16.899	15.861	13.792	10.785
Percentage	33.147	17.819	12.970	9.857	5.903	5.253	3.595	3.375	2.934	2.295
Cumulative Percentage	33.147	50.966	63.935	73.792	79.695	84.948	88.544	91.918	94.853	97.147

	11	12	13	14	15	16	17	18	19	20
Atopina antiqua	0.061	-0.330	0.061	-0.103	-0.007	-0.029	-0.373	-0.113	0.059	0.052
Atops rupertensis	0.153	-0.830	0.259	0.071	0.119	-0.113	0.267	-0.107	-0.069	-0.002
A. trilineatus	-0.314	0.414	-0.293	-0.400	0.152	-0.355	-0.348	0.277	0.062	-0.072
Bailiaspis bobrovi	-0.108	0.345	-0.566	0.746	-0.209	-0.509	0.199	-0.363	0.000	0.006
B. dalmani	0.431	0.040	-0.836	-0.944	0.160	0.240	-0.278	-0.271	-0.055	-0.175
B. glabrata	-0.936	0.270	0.012	-0.387	0.061	-0.334	0.323	-0.624	0.045	0.229
B. venusta	0.410	0.013	-0.486	-0.111	0.628	0.256	0.458	0.159	-0.018	-0.108
Bailiella aequalis	0.574	-0.516	0.478	-0.411	1.036	0.254	-0.014	-0.090	-0.213	0.098
B. baileyi	-0.436	0.784	0.029	0.169	0.274	0.066	0.291	0.592	0.457	-0.436
B. emarginata	-0.096	0.217	0.157	-0.052	-0.288	0.317	-0.279	0.337	-0.281	0.317
B. lantenoisi	-0.508	0.036	-0.222	0.263	0.020	0.555	0.569	0.051	0.549	0.043
B. levyi	-0.708	-0.068	0.976	-0.192	0.373	-0.299	-0.186	-0.585	0.031	-0.055
Conocoryphe caecigena	0.148	-0.731	-0.324	0.768	-0.006	0.189	-0.781	0.175	0.247	-0.459
C. sulzeri	0.536	0.848	0.061	0.038	-0.814	-0.037	0.102	-0.049	-0.732	-0.356
Cornucoryphe schirmi	-1.063	-0.997	-0.265	-0.371	-0.596	-0.473	0.078	0.582	-0.391	0.290
Couloumania heberti	1.023	0.015	-0.089	0.723	-0.261	0.024	0.205	0.020	-0.066	0.564
Ctenocephalus (C.) bergeroni	-0.121	0.428	-0.073	0.143	0.567	0.440	-0.239	0.431	-0.107	0.040
C. (C.) coronatus	-0.332	0.238	-0.394	-0.156	0.370	-0.130	-0.625	-0.678	-0.114	-0.084
C. (Hartella) antiquus	0.269	-0.101	0.239	-0.180	-0.117	-0.062	0.143	-0.149	0.164	0.007
C. (H.) exsulans	-0.388	-0.249	-0.554	-0.161	-0.832	-0.006	-0.520	-0.053	0.322	-0.033
C. (H.) matthewi	0.193	-0.021	0.353	-0.677	0.265	-0.419	0.650	0.450	0.191	0.294
C. (H.) terranovicus	-0.061	-0.332	-0.348	-0.160	0.317	-0.093	0.325	-0.154	-0.491	-0.272
Dasometopus breviceps	0.312	0.351	0.202	0.104	0.311	-0.126	-0.340	0.047	-0.098	0.271
D. granulatus	0.311	-0.024	0.058	0.473	-0.103	-0.898	0.401	0.218	-0.241	-0.099
D. maensis	-0.021	-0.115	-0.460	-0.643	-0.454	0.419	0.241	-0.167	-0.261	-0.201
Elyx laticeps	-0.278	0.472	0.347	0.725	0.496	-0.529	-0.276	-0.216	-0.112	0.074
E. matthewi	-0.215	-0.889	0.416	-0.046	-0.270	0.372	0.212	0.004	0.370	-0.020
Hartshillia clivosa	-0.769	-0.019	-0.009	0.280	0.031	-0.558	0.180	0.330	-0.105	-0.409
H. inflata	0.792	-0.150	-0.329	0.336	-0.147	-0.039	0.244	-0.621	0.406	0.114
Hartshillina spinata	0.199	0.208	0.285	-0.224	0.186	0.130	-0.013	0.224	-0.098	0.032
Holocephalina laxa	0.145	-0.607	-0.338	0.580	-0.239	0.503	0.225	-0.176	-0.578	0.002
H. primordialis	1.204	0.201	0.583	-0.689	-0.261	-0.531	-0.241	0.083	0.368	-0.330
Holocephalites incertus	-0.102	0.184	-0.530	-0.270	0.335	0.265	-0.091	0.382	0.079	-0.023
Meneviella venulosa	-0.198	0.008	-0.801	0.270	0.359	-0.265	-0.240	0.117	0.407	0.471
M. viatrix	-0.615	-0.305	1.047	0.314	-0.166	0.476	-0.046	-0.247	0.086	-0.281
Parabailiella languedocensis	0.648	-0.159	0.171	-0.047	-0.481	-0.199	-0.188	0.131	0.328	0.068
Pseudatops reticulatus	-0.396	0.862	0.002	-0.197	-0.508	0.548	0.523	-0.458	0.163	0.146
Sdzuyella stremina	-0.214	0.337	0.543	-0.148	-0.376	0.345	-0.598	0.178	-0.251	0.519
Tchaiaspis sdzuyi	-0.009	0.394	0.429	0.504	-0.125	0.648	-0.007	0.311	-0.077	-0.096
Tchaiaspis sp. nov.	0.473	-0.221	0.214	0.062	-0.275	-0.064	0.048	0.020	0.021	-0.122
Eigenvalues	9.852	7.606	7.392	6.725	6.103	5.412	4.610	4.091	3.164	2.357
Percentage	2.096	1.618	1.573	1.431	1.299	1.151	0.981	0.870	0.673	0.501
Cumulative Percentage	99.243	100.86	102.43	103.87	105.16	106.32	107.30	108.17	108.84	109.34

	21	22	23	24	25	26	27	28	29	30
Atopina antiqua	-0.057	0.142	-0.014	0.165	-0.035	-0.032	0.006	0.003	0.031	0.026
Atops rupertensis	-0.290	-0.133	-0.161	0.091	0.278	-0.050	-0.004	0.002	0.093	-0.166
A. trilineatus	0.534	0.025	-0.141	0.027	-0.089	-0.038	-0.005	0.002	-0.115	0.027
Bailiaspis bobrovi	0.135	0.026	-0.082	-0.030	-0.129	0.092	0.013	0.003	0.040	-0.306
B. dalmani	-0.349	-0.205	-0.128	-0.106	-0.046	-0.276	-0.014	0.002	-0.035	-0.142
B. glabrata	-0.103	0.084	-0.039	0.186	0.140	0.077	-0.015	0.002	-0.072	0.065
B. venusta	-0.255	-0.032	0.062	-0.064	-0.155	0.185	-0.007	0.002	-0.023	0.086
Bailiella aequalis	0.385	-0.127	0.083	-0.134	0.061	0.178	0.027	0.004	0.021	-0.066
B. baileyi	0.017	-0.170	0.194	-0.082	0.247	-0.053	0.008	0.003	0.035	0.014
B. emarginata	0.517	0.188	-0.074	0.197	0.255	-0.121	-0.008	0.002	-0.094	0.042
B. lantenoisi	0.192	-0.128	-0.183	0.156	-0.293	-0.181	0.015	0.003	0.033	-0.002
B. levyi	-0.083	0.011	-0.069	-0.209	-0.020	0.011	-0.014	0.002	0.152	0.095
Conocoryphe caecigena	-0.355	0.189	-0.006	0.116	-0.001	0.150	-0.017	0.002	-0.090	0.107
C. sulzeri	-0.022	0.373	-0.173	0.078	0.034	0.092	0.002	0.003	0.115	-0.113
Cornucoryphe schirmi	-0.366	0.115	-0.045	-0.090	-0.038	-0.031	0.009	0.003	-0.052	0.034
Couloumania heberti	-0.005	-0.527	-0.251	-0.208	0.111	0.013	-0.020	0.002	-0.095	0.140
Ctenocephalus (C.) bergeroni	-0.179	0.061	-0.240	0.169	-0.139	0.092	-0.007	0.002	0.113	-0.017
C. (C.) coronatus	0.188	0.039	0.069	-0.164	-0.061	-0.022	-0.009	0.002	-0.147	-0.181
C. (Hartella) antiquus	-0.294	0.049	0.007	-0.016	0.077	-0.055	0.044	0.004	-0.153	0.115
C. (H.) exsulans	0.175	-0.535	0.014	-0.074	0.079	0.056	-0.003	0.003	0.197	0.043
C. (H.) matthewi	-0.088	0.042	0.039	0.261	-0.015	0.035	-0.027	0.001	-0.004	-0.242
C. (H.) terranovicus	0.174	0.110	0.087	0.088	-0.118	-0.115	-0.009	0.002	0.073	0.512
Dasometopus breviceps	-0.208	0.165	-0.075	-0.100	-0.014	-0.257	0.004	0.003	0.106	-0.071
D. granulatus	0.129	-0.124	-0.014	-0.147	-0.329	0.007	-0.008	0.002	-0.049	0.060
D. maensis	0.054	-0.262	0.079	0.156	0.088	0.237	0.006	0.003	-0.041	-0.031
Elyx laticeps	-0.153	-0.250	0.241	0.226	0.104	0.060	-0.008	0.002	-0.042	0.039
E. matthewi	0.391	0.395	-0.109	-0.303	-0.030	0.111	-0.021	0.002	0.001	-0.104
Hartshillia clivosa	0.046	-0.115	-0.041	-0.148	0.156	-0.039	0.000	0.003	-0.025	-0.112
H. inflata	0.035	0.204	-0.142	0.207	0.019	-0.010	-0.002	0.003	0.011	0.007
Hartshilina spinata	-0.088	-0.056	0.078	-0.142	-0.024	-0.019	-0.011	0.002	0.007	0.018
Holocephalina leve	0.127	0.051	0.246	-0.037	0.082	-0.125	-0.004	0.002	0.018	-0.150
H. primordialis	0.009	0.047	-0.244	-0.036	0.038	0.044	0.001	0.003	-0.020	0.121
Holocephalites incertus	-0.004	-0.034	0.012	0.038	0.002	0.064	-0.014	0.002	-0.003	-0.087
Meneviella venulosa	0.035	0.396	-0.018	-0.060	0.144	0.066	0.008	0.003	0.072	0.149
M. viatrix	-0.035	-0.205	-0.146	0.204	-0.164	-0.070	-0.003	0.002	-0.089	-0.060
Parabailiella languedocensis	-0.067	0.162	0.682	0.018	-0.154	-0.062	-0.005	0.002	0.005	-0.145
Pseudatops reticulatus	-0.224	0.154	0.226	-0.227	0.028	0.035	-0.011	0.002	-0.020	0.146
Sdzuyella stremina	-0.069	-0.203	0.095	0.036	-0.245	0.121	0.007	0.003	0.026	0.028
Tchaiaspis sdzuyi	-0.153	0.184	-0.073	-0.196	0.087	-0.037	-0.005	0.002	-0.071	0.005
Tchaiaspis sp. nov.	0.306	-0.103	0.260	0.155	0.075	-0.135	-0.011	0.002	0.051	0.116
Eigenvalues	1.977	1.690	1.182	0.873	0.733	0.482	0.006	0.000	-0.242	-0.744
Percentage	0.421	0.360	0.252	0.186	0.156	0.103	0.001	0.000	0.051	0.158
Cumulative Percentage	109.76	110.12	110.37	110.56	110.71	110.82	110.82	110.82	110.87	111.03

	31	32	33	34	35	36	37	38	39	40
Atopina antiqua	-0.125	-0.198	0.103	-0.049	0.216	-0.092	-0.113	-0.438	-1.763	0.680
Atops rupertensis	-0.161	-0.059	-0.050	-0.371	-0.541	0.105	0.133	0.080	0.433	-0.433
A. trilineatus	0.434	0.315	0.184	0.065	0.190	0.209	0.256	-0.562	0.225	-0.655
Bailiaspis bobrovi	-0.160	-0.123	0.175	-0.062	0.559	0.107	0.278	0.774	0.061	0.283
B. dalmani	-0.099	0.162	-0.066	0.400	-0.207	0.262	-0.108	0.027	0.366	0.374
B. glabrata	0.356	-0.306	-0.024	0.018	-0.507	0.273	0.376	-0.230	-0.329	0.492
B. venusta	0.251	-0.047	-0.039	-0.409	0.257	-0.726	-0.330	0.077	0.174	-0.022
Bailiella aequalis	0.086	-0.167	-0.009	0.329	-0.167	-0.172	-0.082	-0.231	0.561	0.401
B. baileyi	-0.172	-0.281	0.023	-0.097	0.318	0.750	-0.035	-0.521	0.093	-0.386
B. emarginata	-0.252	0.034	0.144	-0.093	-0.012	-0.230	-0.457	0.891	0.284	0.440
B. lantenoisi	-0.159	0.119	-0.214	-0.130	-0.454	-0.414	0.207	-0.228	-0.364	-0.300
B. levyi	-0.151	0.471	0.312	0.013	0.296	0.057	-0.124	0.227	-0.133	-0.615
Conocoryphe caecigena	-0.092	0.179	-0.208	-0.069	0.126	0.044	0.230	-0.249	0.332	0.458
C. sulzeri	0.169	0.116	-0.243	-0.227	-0.261	-0.094	-0.094	-0.405	0.057	-0.874
Cornucoryphe schirmi	0.038	-0.291	-0.009	0.275	0.339	-0.065	-0.306	-0.095	0.201	-0.711
Couloumania heberti	0.059	-0.013	0.051	-0.005	0.157	0.015	0.567	0.014	-0.383	-0.669
Ctenocephalus (C.) bergeroni	0.084	-0.103	-0.038	0.807	-0.054	0.266	0.071	0.736	-0.395	0.072
C. (C.) coronatus	-0.304	-0.284	-0.197	-0.301	-0.007	-0.308	-0.136	-0.247	-0.159	-0.538
C. (Hartella) antiquus	0.165	0.400	-0.137	-0.283	0.057	0.370	-0.192	0.579	-0.236	0.327
C. (H.) exsulans	0.276	-0.006	0.187	-0.189	-0.078	-0.233	-0.591	-0.092	-0.017	0.709
C. (H.) matthewi	-0.160	0.270	0.084	-0.168	0.401	-0.211	-0.107	-0.506	-0.008	0.672
C. (H.) terranovicus	-0.154	-0.141	0.287	-0.305	0.031	0.107	0.504	0.230	0.374	0.312
Dasometopus breviceps	0.251	-0.144	-0.153	-0.280	0.382	-0.048	0.524	-0.220	0.350	0.629
D. granulatus	-0.150	0.029	-0.035	0.127	-0.521	0.454	-0.715	-0.172	-0.084	0.619
D. maensis	-0.272	0.171	0.155	0.222	0.144	0.138	0.532	-0.177	-0.226	-0.589
Elyx laticeps	0.061	0.101	-0.184	0.095	-0.179	-0.004	-0.318	0.088	-0.053	0.130
E. matthewi	0.082	-0.017	-0.363	-0.088	-0.057	0.509	0.195	0.185	-0.091	0.427
Hartshillia clivosa	-0.008	0.136	-0.100	0.304	-0.165	-0.729	0.610	0.275	0.221	0.949
H. inflata	-0.004	-0.136	0.252	0.295	0.233	0.210	-0.488	-0.348	1.066	-0.052
Hartshillina spinata	-0.090	-0.092	-0.163	-0.067	-0.028	0.018	-0.252	0.203	-0.330	-1.993
Holocephalina leve	0.208	0.212	0.131	0.074	0.144	0.219	-0.161	-0.279	-0.902	0.285
H. primordialis	-0.062	-0.217	0.074	0.082	-0.037	-0.261	0.112	0.268	-0.579	0.310
Holocephalites incertus	0.153	-0.058	0.056	-0.608	-0.168	0.336	-0.226	0.888	-0.072	0.131
Meneviella venulosa	-0.133	0.208	-0.042	0.136	-0.313	-0.242	-0.025	-0.237	0.018	-1.212
M. viatrix	0.214	-0.159	0.157	0.016	0.181	-0.186	-0.148	0.173	0.386	-1.095
Parabailiella languedocensis	0.129	-0.038	0.436	0.140	-0.423	-0.095	0.510	0.425	0.097	-0.700
Pseudatops reticulatus	-0.025	0.017	-0.215	0.293	0.166	-0.240	-0.182	0.232	0.146	0.710
Sdzuyella stremina	-0.236	0.047	-0.200	-0.258	-0.077	0.304	0.352	-0.421	0.630	0.839
Tchaiaspis sdzuyi	-0.063	-0.057	0.617	0.065	-0.282	-0.246	-0.176	-0.677	0.015	0.705
Tchaiaspis sp. nov.	0.038	-0.035	-0.742	0.303	0.331	-0.159	-0.095	-0.036	0.033	-0.110
Eigenvalues	-1.286	-1.377	-2.109	-2.742	-3.015	-3.618	-4.312	-6.168	-8.073	-17.16
Percentage	0.274	0.293	0.449	0.583	0.642	0.770	0.918	1.312	1.718	3.651
Cumulative Percentage	111.3	111.59	112.04	112.63	113.27	114.04	114.96	116.27	117.99	121.64

Appendix 5. Characters and character states used in phylogenetic analysis of Arachnomorpha in Part 3.

1. Appendages of the first segment (antennae). 0: Present, 1: Absent.
2. Form of endopod of appendages of the second segment. 0: Pediform, 1: Anteriorly directed raptorial appendage with reduced number of podomeres and terminal podomeres bearing spines on distal margins.
3. Exopod of appendages of the second segment. 0: Present, 1: Absent or much reduced.
4. Number of segments incorporated into the head. 0: 1, 1: 2, 2: 3, 3: 4, 4: 5, 5: 6, 6: 7.
5. Orientation of the antennae. 0: Directed anterolaterally, 1: Strongly deflected laterally, 2: Placed well inside shield margin, curving posteriorly from a transverse proximal element.
6. Length of distal spines on terminal podomeres of endopods of second segment appendages. 0: Absent or shorter than podomeres, 1: Subequal to length of podomeres, 2: Longer than the entire podomere series.
7. Chelicerae. 0: Absent, 1: Present.
8. Distal spines of second segment endopods terminating in annulated flagellae. 0: Absent, 1: Present.
9. Appendages of first thoracic somite underneath the cephalo-thoracic articulation. 0: Absent, 1: Present.
10. Exopods of appendages of third to fifth segments. 0: Present, 1: Reduced or absent.
11. Endopods of thoracic appendages. 0: Present, 1: Reduced or absent.
12. Exopod shaft of numerous podomeres, each bearing a single seta. 0: Present, 1: Absent.
13. Exopod shaft differentiated into proximal and distal lobes. 0: Absent, 1: Present.
14. Proximal lobe of exopod. 0: Flattened lobe, 1: Slender shaft.
15. Distal lobe of exopod. 0: Small to moderate sized flap, with short to moderately long attachment to proximal lobe, 1: Large, teardrop shaped, with long attachment to proximal lobe.
16. Exopod shaft a deep rounded flap. 0: Absent, 1: Present.
17. Medially directed exopod setae. 0: Absent, 1: Present.
18. Lamellate exopod setae. 0: Absent, 1: Present.
19. Gnathobase on basis and/or prominent endites on endopod. 0: Present, 1: Absent.
20. Position of lateral facetted eyes. 0: Ventral and stalked, 1: Dorsal and sessile, 2: Absent.
21. Visual surface with calcified lenses, bounded with circumocular suture. 0: Absent, 1: Present.
22. Dorsal bulge in exoskeleton accommodating drop-shaped ventral eyes. 0: Absent, 1: Present.
23. Eye slits. 0: Absent, 1: Present.
24. Dorsal median eyes. 0: Absent, 1: Present.
25. Expanded cephalic doublure. 0: Absent, 1: Present, maximum width more than 30 percent length of head shield or more than 25 percent width of pygidium.
26. Anteromedian margin of cephalon notched, accomodating strongly sclerotised plate. 0: Notch and plate absent, 1: Notch and plate present.
27. Hypostomal sclerite. 0: Median extension of the doublure, with no suture, 1: Natant, sclerite not in contact with doublure, 2: With narrow overlap with pre-hypostomal sclerite, 3: Narrow attachment to doublure at hypostomal suture; 4: Absent.

28. Visible ecdysial sutures. 0: Absent; 1: Present.
29. Position of ecdysial sutures. 0: Marginal; 1: Dorsal.
30. Mineralised cuticle. 0: Absent; 1: Present.
31. Trunk tergites with expanded lateral pleurae covering appendages dorsally. 0: Absent, 1: Present.
32. Free thoracic tergites. 0: Present, 1: Absent.
33. Decoupling of thoracic tergites and segments. 0: Absent, 1: Present.
34. Tergite articulations. 0: Tergites non-overlapping, 1: Extensive overlap of tergites, 2: Edge-to-edge pleural articulations.
35. Trunk effacement. 0: Trunk with defined (separate or fused) tergite boundaries, 1: Trunk tergite boundaries effaced laterally, 2: Trunk tergite boundaries completely effaced.
36. Cephalic articulation fused. 0: Absent, 1: Present.
37. Head shield overlap of thoracic tergites: 0- overlap absent or identical to overlap between thoracic segments. 1: Head shield covers first thoracic tergite only, 2: Head shield covers mutliple anterior trunk tergites.
38. Head shield articulates with reduced anterior thoracic tergite. 0: Absent, 1: Present.
39. Trunk narrowed anteriorly relative to head shield, widest posteriorly. 0: Absent, 1: Present.
40. Boundaries of anterior trunk segments reflexed anterolaterally. 0: Absent, boundaries transverse or reflexed posterolaterally, 1: Present.
41. Joints between posterior tergites functional, anterior ones variably fused. 0: Absent, 1: Present.
42. Posterior tergite bearing axial spine. 0: Absent; 1: Present.
43. Postabdomen of segments lacking appendages. 0: Absent, 1: Present.
44. Length of postabdomen. 0: 1 segment, 1: 2 segments, 2: 3 segments, 3: 5 segments.
45. Posterior tergites strongly curved in dorsal aspect compared to anterior tergites. 0: Absent, 1: Present.
46. Posterior segments reduced and with highly reduced appendages. 0: Present, 1: Absent.
47. Pygidium. 0: Absent, 1: Present.
48. Position of the anus. 0: Terminal, within telson, 1: At base of telson.
49. Pygidium with median keel. 0: Absent, 1: Present.
50. Pygidium with broad-based median spine. 0: Absent, 1: Present.
51. Pygidium with lateral spines. 0: Present, 1: Absent.
52. Expanded post-segmental telson. 0: Absent, 1: Present.
53. Telson shape. 0: Spinose, 1: Paddle-shaped.
54. Post-ventral furcae, 0: Absent, 2: Present.

Appendix 6. PAUP command files used to test the fit of head segmentation to phylogeny in Part 3.

Character coding and topology based on (1) the analysis of arachnomorph phylogeny herein, (2) the analysis of arthropod phylogeny by Wills *et al.* (1998*a*), (3) the phylogeny of the arachnomorph clade only from Wills *et al.* (1998*a*).

1. Arachnomorpha (herein)

```
BEGIN DATA;
DIMENSIONS,NTAX=33 NCHAR=1;
FORMAT SYMBOLS= " 0 1 2 3 4 5 6" MISSING=? GAP=-
;OPTIONS,MSTAXA=UNCERTAIN ;
MATRIX
OUTGROUP,0
Aglaspidida2,,,,,{34}
Alalcomenaeus,,,, 3
Buenaspis,,,,,, ?
Burgessia,,,,,, 3
Cheloniellon,,,,,4
Cindarella,,,,,,6
Crustacea,,,,,, 3
Emeraldella,,,,, 5
Eoredlichia,,,,, 3
Eurypterida,,,,, 6
Fortiforceps,,,,,4
HelmetiaKuamaia,,, 3
Jianfengia,,,,,,4
Leanchoilia,,,,, 3
Lemoneites,,,,,,?
Liwia,, ?
Marrella,1
Mimetaster,,,,,,2
Misszhouia,,,,,,3
Naraoia, 3
Olenoides,,,,,, ?
Paleomerus,,,,,,?
Pycnogonida,,,,, 4
Retifacies,,,,,,3
SaperionSkioldia,,,?
Sidneyia,0
Sinoburius,,,,,,4
SoomaspisTariccoia,,?
Tegopelte,,,,,, ?
Weinbergina,,,,, 6
Xandarella,,,,,,4
Yohoia,,4
;
END;
BEGIN ASSUMPTIONS;
usertype head = 7
0 1 2 3 4 5 6
. 1 2 3 4 5 6
1 . 1 2 3 4 5
2 1 . 1 2 3 4
3 2 1 . 1 2 3
4 3 2 1 . 1 2
5 4 3 2 1 . 1
```

```
6 5 4 3 2 1 .
;
END;
BEGIN PAUP;
constraint Strict =,[&U]
(OUTGROUP,(((((Aglaspidida2,Cheloniellon,Emeraldella,Lemoneites,Paleom
erus,Sidneyia),(((Alalcomenaeus,Leanchoilia),(((Eurypterida,Weinbergin
a),Pycnogonida),Yohoia),Jianfengia),Fortiforceps)),(((((Buenaspis,(Liw
ia,SoomaspisTariccoia)),(Misszhouia,Naraoia)),((Eoredlichia,Olenoides)
,(HelmetiaKuamaia,(SaperionSkioldia,Tegopelte)))),((Cindarella,Xandare
lla),Sinoburius)),Retifacies)),Burgessia),Crustacea),(Marrella,Mimetas
ter));
constraint Chosen = [&U]
(OUTGROUP,(((((((((Aglaspidida2,(Lemoneites,Paleomerus)),Cheloniellon)
,Sidneyia),Emeraldella),(((Alalcomenaeus,Leanchoilia),(((Eurypterida,W
einbergina),Pycnogonida),Yohoia),Jianfengia),Fortiforceps)),(((((Buena
spis,(Liwia,SoomaspisTariccoia)),(Misszhouia,Naraoia)),((Eoredlichia,O
lenoides),(HelmetiaKuamaia,(SaperionSkioldia,Tegopelte)))),((Cindarell
a,Xandarella),Sinoburius)),Retifacies)),Burgessia),Crustacea),(Marrell
a,Mimetaster)));
constraint NoHeadStrict = [&U]
(OUTGROUP,((((Aglaspidida2,Cheloniellon,Emeraldella,Lemoneites,Paleome
rus,Sidneyia),(((Alalcomenaeus,Leanchoilia),(((Eurypterida,Weinbergina
),Pycnogonida),Yohoia),Jianfengia),Fortiforceps)),(((Buenaspis,(Liwia,
SoomaspisTariccoia)),(Misszhouia,Naraoia)),((Eoredlichia,Olenoides),(H
elmetiaKuamaia,(SaperionSkioldia,Tegopelte)))),((Cindarella,Xandarella
),Sinoburius),Retifacies),Burgessia,Crustacea,(Marrella,Mimetaster)));
log file=headtest(chosen)20000.log;
set autoclose;
ctype head : 1;
hsearch enforce constraints=Chosen;
pscore;
permute randomize=all nreps=20000;
log stop;
END;
```

2. Arthropoda (from Wills *et al.*, 1998*a*)

```
#NEXUS
BEGIN DATA;
DIMENSIONS NTAX=63,NCHAR=1;
FORMAT MISSING=?;
FORMAT SYMBOLS="0~9";
MATRIX
Acerentomon,,,,,, 5
Aglaspis,,4
Agnostus,,4
Alalcomenaeus,,,,, 4
Alima,,, 5
Androctonus,,,,,, 6
Anomalocaris,,,,,,4
Argulus,, 5
Artemia,, 5
Aysheaia,,1
Baltoeurypterus,,,, 6
Branchiocaris,,,,, 2
Bredocaris,5
Burgessia, 4
Calanus,, 5
Campodea,,5
```

```
Canadaspis,5
Cheloniellon,,,,,,6
Corynothrix,,,,,, 5
Cypridina, 5
Derocheilocaris,,,, 5
Echiniscus,1
Emeraldella,,,,,, 6
Galathea,,5
Habelia,, 3
Julus,,, 4
Kalbarria, 3
Kerygmachela,,,,,,1
Leanchoilia,,,,,, 3
Lepas,,, 5
Lepidocaris,,,,,, 5
Lepidurus, 5
Lepisma,, 5
Lithobius, 5
Marrella,,2
Martinssonia,,,,,,5
Mimetaster,3
Molaria,, 4
Nahecaris, 5
Naraoia,, 4
Nebalia,, 5
Odaraia,, 5
Olenoides, 4
Opabinia,,1
Pauropus,,4
Peripatoides,,,,,,3
Periplaneta,,,,,, 5
Perspicaris,,,,,, 5
Rehbachiella,,,,,,5
Sanctacaris,,,,,, 6
Sandersiella,,,,,,5
Sarotrocercus,,,,, 2
Scutigerella,,,,,,5
Sidneyia,,1
Skara,,, 5
Speleonectes,,,,,,5
Tachypleus,6
Triarthrus,4
Vachonisia,4
Waptia,,,5
Weinbergina,,,,,, 7
Yohoia,,,4
OUTGROUP,,0
;
END;
BEGIN ASSUMPTIONS;
usertype head = 8
0 1 2 3 4 5 6 7
. 1 2 3 4 5 6 7
1 . 1 2 3 4 5 6
2 1 . 1 2 3 4 5
3 2 1 . 1 2 3 3
4 3 2 1 . 1 2 3
5 4 3 2 1 . 1 2
6 5 4 3 2 1 . 1
7 6 5 4 3 2 1 .
;
```

```
END;
BEGIN PAUP;
constraint majrule = [&U]
(((((((Acerentomon,Campodea),(((Corynothrix,Lepisma),Periplaneta),Kal
barria)),((Julus,Pauropus),(Lithobius,Scutigerella))),(((((((Aglaspis,
((((Androctonus,Baltoeurypterus),Tachypleus),Weinbergina),Cheloniellon
)),(((Alalcomenaeus,(Sanctacaris,Yohoia)),((Habelia,Leanchoilia),Sarot
rocercus)),Sidneyia)),Emeraldella),(((Agnostus,(Olenoides,Triarthrus))
,Naraoia),Molaria)),Burgessia),((((((((((Alima,Galathea),Nebalia),Na
hecaris),Cypridina),((Canadaspis,Odaraia),Perspicaris)),Waptia),(Artem
ia,Lepidurus)),(Bredocaris,Rehbachiella)),Sandersiella),Lepidocaris),(
(((Argulus,Lepas),Calanus),Derocheilocaris),(Martinssonia,Skara))),Spe
leonectes)),(Branchiocaris,((Marrella,Mimetaster),Vachonisia)))),Echin
iscus),((Aysheaia,Kerygmachela),Peripatoides)),(Anomalocaris,Opabinia)
),OUTGROUP);
constraint strict = [&U]
(((((Acerentomon,Campodea,((Corynothrix,Lepisma),Periplaneta),((Julus
,Pauropus),Lithobius,Scutigerella),Kalbarria),(((Aglaspis,((((Androcto
nus,Baltoeurypterus),Tachypleus),Weinbergina),Cheloniellon)),((Agnostu
s,(Olenoides,Triarthrus)),Naraoia),Alalcomenaeus,Emeraldella,(Habelia,
Leanchoilia),Molaria,Sanctacaris,Sarotrocercus,Sidneyia,Yohoia),(((((A
lima,Galathea),Nebalia),Nahecaris),Cypridina),Canadaspis,Odaraia,Persp
icaris),(Argulus,Lepas),(Artemia,Lepidurus),Branchiocaris,(Bredocaris,
Rehbachiella),Burgessia,Calanus,Derocheilocaris,Lepidocaris,(Marrella,
Mimetaster,Vachonisia),(Martinssonia,Skara),Sandersiella,Speleonectes,
Waptia)),Echiniscus),(Aysheaia,Kerygmachela,Peripatoides)),(Anomalocar
is,Opabinia)),OUTGROUP);
constraint 75majrule = [&U]
(((((((Acerentomon,Campodea),(((Corynothrix,Lepisma),Periplaneta),Kal
barria)),((Julus,Pauropus),(Lithobius,Scutigerella))),(((((((Aglaspis,
((((Androctonus,Baltoeurypterus),Tachypleus),Weinbergina),Cheloniellon
)),(((Alalcomenaeus,(Sanctacaris,Yohoia)),((Habelia,Leanchoilia),Sarot
rocercus)),Sidneyia)),Emeraldella),(((Agnostus,(Olenoides,Triarthrus))
,Naraoia),Molaria)),Burgessia),((((((((((Alima,Galathea),Nebalia),Na
hecaris),Cypridina),((Canadaspis,Odaraia),Perspicaris)),Waptia),(Artem
ia,Lepidurus)),(Bredocaris,Rehbachiella)),Sandersiella),Lepidocaris),(
(((Argulus,Lepas),Calanus),Derocheilocaris),(Martinssonia,Skara))),Spe
leonectes)),(Branchiocaris,((Marrella,Mimetaster),Vachonisia)))),Echin
iscus),((Aysheaia,Kerygmachela),Peripatoides)),(Anomalocaris,Opabinia)
),OUTGROUP);
log file=headtestMAW(majrule)20000.log;
set autoclose;
ctype head : 1;
hsearch enforce constraints=majrule;
pscore;
permute randomize=all nreps=20000;
log stop;
END;
```

3. Arachnomorpha (from Wills *et al.*, 1998*a*)

```
#NEXUS
BEGIN DATA;
DIMENSIONS NTAX=20,NCHAR=1;
FORMAT MISSING=?;
FORMAT SYMBOLS="0~9";
MATRIX
Aglaspis,,4
```

```
Agnostus,,4
Alalcomenaeus,,,,, 4
Androctonus,,,,,, 6
Baltoeurypterus,,,, 6
Burgessia, 4
Cheloniellon,,,,,,6
Emeraldella,,,,,, 6
Habelia,, 3
Leanchoilia,,,,,, 3
Molaria,, 4
Naraoia,, 4
Olenoides, 4
Sanctacaris,,,,,, 6
Sarotrocercus,,,,, 2
Sidneyia,,1
Tachypleus,6
Triarthrus,4
Weinbergina,,,,,, 7
Yohoia,,,4
;
END;
BEGIN ASSUMPTIONS;
usertype head = 8
0 1 2 3 4 5 6 7
. 1 2 3 4 5 6 7
1 . 1 2 3 4 5 6
2 1 . 1 2 3 4 5
3 2 1 . 1 2 3 3
4 3 2 1 . 1 2 3
5 4 3 2 1 . 1 2
6 5 4 3 2 1 . 1
7 6 5 4 3 2 1 .
;
END;
BEGIN PAUP;
constraint majrule = [&U]
(((((Aglaspis,((((Androctonus,Baltoeurypterus),Tachypleus),Weinbergina
),Cheloniellon)),(((Alalcomenaeus,(Sanctacaris,Yohoia)),((Habelia,Lean
choilia),Sarotrocercus)),Sidneyia)),Emeraldella),(((Agnostus,(Olenoide
s,Triarthrus)),Naraoia),Molaria)),Burgessia);
constraint strict = [&U]
((Aglaspis,((((Androctonus,Baltoeurypterus),Tachypleus),Weinbergina),C
heloniellon)),((Agnostus,(Olenoides,Triarthrus)),Naraoia),Alalcomenaeu
s,Emeraldella,(Habelia,Leanchoilia),Molaria,Sanctacaris,Sarotrocercus,
Sidneyia,Yohoia);
constraint 75majrule = [&U]
(((((Aglaspis,((((Androctonus,Baltoeurypterus),Tachypleus),Weinbergina
),Cheloniellon)),(((Alalcomenaeus,(Sanctacaris,Yohoia)),((Habelia,Lean
choilia),Sarotrocercus)),Sidneyia)),Emeraldella),(((Agnostus,(Olenoide
s,Triarthrus)),Naraoia),Molaria)),Burgessia);
log file=headtestMAWAr(majrule)20000.log;
set autoclose;
ctype head : 1;
hsearch enforce constraints=majrule;
pscore;
permute randomize=all nreps=20000;
log stop;
END;
```

Appendix 7. Character distribution matrix used in the analysis of eodiscinid phylogeny following Jell.

All characters are as described by Jell (1975, Appendix A), except Character 14, ratio of width of pygidial axis to pleura, coded as 0: up to 0.75, 1: 0.75-0.99, 2: 1.00-1.10, 3: 1.11-1.20, 4: 1.21-1.30 and 5: >1.30. Letters indicate multistate coding, as follows: A = (12), B = (23), C = (34), D = (13), E = (24), F = (14), G = (234), H=(345), I=(123), J=(124), K=(356), L=(126), M=(1234), N=(2345).

TAXON	CHARACTERS 1111111111222222222233333333334 12345678901234567890123456789012345678901234567890
Acidiscus	00101110000001323132121122413121 2B112331
Leptochilodiscus	001000000000?45131211231?241314141323112
Litometopus	001000000000?33113261231?211314332334111
Cobboldites	00100000100004411126423122313113211121 11
Serrodiscus	00100100000002HAADG2D2D3224A31D1E132E131
Mensicuchus	00100000000104342346451221113111411431 41
Stigmadiscus	00001110100 0?04231C1A223?242321121223131
Ladadiscus	00100000001002C131224433224133142111211 1
Metadiscus	00100000000000313121423121413111411111 11
Bolboparia	001000100001?35232221321?243313242124141
Analox	011000100001?23331452315?2313143?1145122
Serrodiscus daedalus	001000000010?33323424233?241331121112141
Bathydiscus	001000000000?56123114211?311412131233113
Oodiscus	001000000000?56121164211?31143112I211111
Tannudiscus	00100000000002632DC6323222113311311111 21
Acimetopus	001000100000?36431461332?243413142114131
Weymouthia	00100000000000?111??241312?11131321112111
Calodiscus	00100000100001K43BGL32DB22214AA341113131
Chelediscus	00101000100001533221123111214113 4A113321
Neocobboldia	10100001110002322 3B13213322A421311113131
Kiskinella	1010000111 00?14222B43534?131413111113211
Dawsonia	00100001100010322 2B435341131413141113211
Eodiscus	00100001100010H222B3A31222C141JD11113131
Pagetia	10111001110010NB22B3DB123231CAM1J11FD231
Helepagetia	101110011000?24222233312?221412111111131
Yukonia	10100001100 0?04122213313222241111111311 1
Opsidiscus	10100[illegible]100011C322B3331212214111111D231
Pagetides	10101001110000C222B3351222C141I141114231
Neopagetina	101001001100?04232313312?331411111113131
Delgadella	101000000100012A13B1311222412111211A1111
Parapagetia	101000000110?12233213313?111231121113121
Macannia	10110001110010232233333311314114121113231
Hebediscus	10101001010001B223B1D31322313111E11A3231
Dipharus	101000000100??2323213313??31311141113231

Appendix 8. Character list for investigation of eodiscinid phylogeny following Öpik.

Characters and coding follows the character distribution table of Öpik (1975, text-fig. 6).

1. Relief. 0: Effaced, 1: Semi-effaced, 2: En Grande Tenue.
2. Posession of Eyes: 0. Blind and sutureless, 1. Eyes "degenerate", 2. Eyes and sutures present. [state 2 is an autapomorphy of *Opsidiscus*]
3. Ocular ridges, 0: Absent, 1: Present.
4. Thoracic segments. 0: Three segments, 1: Two segments.
5. Spine on 2nd thoracic segment. 0: Absent, 1: Present.
6. Width of the cephalic rim. 0: Narrow, 1: Medium, 2: Wide.
7. Cephalic rim crescentic. 0: Absent, 1: Present.
8. Median swelling on cephalic rim. 0: Absent, 1: Present.
9. Cephalic rim smooth. 0: Absent, 1: Present.
10. Cephalic rim with nodes. 0: Absent, 1: Present.
11. Cephalic rim venulose. 0: Absent, 1: Present. [autapomorphy of *Discomesites*]
12. Cephalic rim crenelate. 0: Absent, 1: Present.
13. Glabella width. 0: Broad, 1: Slender.
14. Glabellar termination pointed. 0: Absent, 1: Present.
15. Glabellar termination blunt. 0: Absent, 1: Present.
16. Glabellar furrows absent. 0: Absent, 1: Present.
17. Lateral glabellar furrows present. 0: Absent, 1: Present.
18. Number of pairs of transcurrent furrows. 0: None, 1: One, 2: Two
19. Occipital condition. 0: Free, 1: Fused.
20. Glabellar spine. 0: Absent, 1: Present.
21. Occipital spine. 0: Absent, 1: Present.
22. Width of pygidial axis. 0: Stout, 1: Slender.
23. Number of pygidial axial rings. 0: 0, 1: 2 to 4, 2: 5 to 8, 3: 9 and above.
24. Presence of terminal pygidial spine. 0: Absent, 1: Present. [autapomorphic for *Pagetia*]
25. Condition of pleurae. 0: Furrowed, 1: Smooth.
26. Doublure normal. 0: Absent, 1: Normal.
27. Pygidial rim serrate. 0: Absent, 1: Present.

    Öpik (1975) suggested that the presence of a cuffed rim is a modification of the serrate rim, and so taxa with both characters have been coded as state 1 for this character.
28. Pygidial rim spinose in plan. 0: Absent, 1: Present.
29. Pygidial rim cuffed. 0: Absent, 1: Present.

Appendix 9. Character distribution matrix used in the analysis of eodiscinid phylogeny following Öpik. Coding follows the character distribution table of Öpik (1975, text-fig. 6). Characters and character states are described above. Letters indicate multistate coding, as follows: A=(01), B=(12), C=(23).

	CHARACTERS
	11111111112222222222
TAXON	12345678901234567890123456789
Serrodiscus	B0000200010001011B00103000100
Weymouthia	00000200010000010000000000000
Delgadella	02000200100000010000000000000
Pagetiellus	02000200100000010000003000100
Hebediscus	B21000101100A1111011002000100
Meniscuchus	20100210110000100210 00B000101
Analox	200?01000000101001110020001 01
Bathydiscus	100?02001000001000000000000101
Bolboparia	200?01101100010010010030001 00
Acimetopus	200?01101000000002010020000 00
Eodiscus	B0001000000111001011 01C0A1000
Pagetides	B2100211000111001011012 01?000
Neopagetina	221?10001000110010A1012 01?000
Discomesites	221?02110010110010110120110 00
Pagetia	B21A10000001110010?101B111000
Opsidiscus	211?00000001111011110110 1?000
Dawsonia	20011210000111101000112 01?000
Eodiscus borealis	20100000000111001011012 01?000
Kiskinella decora	221?00000001110010110120 1?000
Calodiscus	20000000110000110200001 01?010
Neocobboldia	220A00001000001000001010 1?010
Stigmadiscus	200?00001000?0100000113 01?010

Appendix 10. Characters and character states used in phylogenetic analyses of Agnostida in Part 4. Character state distributions are shown in Table 9. The conditions for characters to be coded as 'not applicable' (see text) are shown in square brackets after the character description. For example, character 2 could only be coded for taxa with a backwardly convex anterior border, coded as state 0 of character 1 (1:0), and is coded as 'not applicable' for taxa with other states of character 1. Autapomorphic characters are indicated in square brackets after the character description. Characters are numbered in approximate order of their position on the eodiscinid body from anterior to posterior, with the exception of characters that are variable only within the agnostid taxa considered (numbers 118 to 123), which are described after other characters.

1. Spines on the posterior cephalic border. 0: Present; 1: Absent.
2. Position and angle of posterior cephalic border spines [1:0]. 0: At genal angles, directed posterolaterally at approximately 45°, 1: Adaxial to genal angles at geniculation, directed posteriorly subparallel to axis.
3. Length of posterior border spine [1:0]. 0: Short (approximately half or less the distance from axial furrows to genal angles), 1: Long (equal to or greater than distance from axial furrows to genal angles).
4. Anterior lateral cephalic border spines. 0: Absent, 1: Present.
5. Angle of anterior lateral cephalic border spines [4:1]. 0: Approximately perpendicular to cephalic axis, 1: Directed anterolaterally at approximately 45 degrees to axis.
6. Posterior lateral cephalic border spines (second pair of spines on the lateral cephalic border). 0: Absent in meraspids and holaspids, 1: Present in meraspids, lost in holaspids, 2: Present in holaspids.
7. Anterior cephalic margin bicuspate in anterior view. 0: Absent, 1: Present.

This character was described in *Leptochilodiscus succinctus* by Bassett, Owens and Rushton (1976). It can also be made out in the type material of *L. punctulatus* Rasetti, 1966 (USNM146009 and USNM 146010), despite dorsoventral flattening.

8. Anterolateral cephalic border scrobiculate. 0: Absent, 1: Present.

Despite Öpik's (1975, p. 33) assertion to the contrary, radial furrows can clearly be seen amongst the tubercles on the anterior cephalic border of at least two specimens of *Discomesite fragum* (Öpik 1975, pl. 5, figs 1, 3). The series of pits on the anterior cephalic border in *Jinghediscus* nummularius Xiang and Zhang, 1985 and *Mallagnostus llarenai* (Richter and Richter 1941) are here treated as homologous with the more fully developed scrobiculae found in other taxa.

9. Depth of cephalic border scrobiculae [8:1]. 0: Very shallow, 1: Moderate, 2: Deep.

10. Length of cephalic border scrobiculae [8:1]: 0: Short (small elongate pits in border furrow), 1: Moderately long (approximately half border width), 2: Long (considerably more than half border width).
11. Epiborder furrow. 0: Absent, 1: Present.
12. Cephalic border nodes. 0: Absent, 1: Present.

The term nodes is used here (following Öpik 1975) for the row of large rounded hollow swellings found on the anterolateral cephalic borders of a range of eodiscinid genera, to distinguish them from the tubercular prosopon of other taxa. Tubercular proson of the anterior border can most easily be distinguished from the border nodes because it is matched by the sculpture of the genae and glabella (see e.g. *Acimetopus bilobatus*, Rasetti 1966, pl. 4, figs 1, 6, 7). The border nodes are likely to have accommodated the ventrally directed spines on the pygidial border during enrollment (Jell *in* Bengtson *et al.* 1990, p. 259). In most taxa the cephalic border nodes form a row of pairs along much of the anterolateral cephalic border. Morphologically similar nodes in *Leptochilodiscus, Bolboparia* and *Ninadiscus* with rather different distributions are treated as homologous, following Jell (*op. cit.*).

13. Number of pairs of border nodes [12:1]. 0: 1-3, 1; 4-6, 2: 7-9, 3: 10+.

This is coded assuming that in species of *Tsunyidiscus* with border nodes the nodes continued onto the free cheeks. The total number of node pairs was therefore estimated from the number on the anterior border (3 pairs in *Tsunyidiscus niutitangensis*, 4 or 5 in *Tsunyidiscus aclis*) and increased in proportion to the length of the free cheek margin. The estimates are 3 or 4 more pairs in *niutitangensis*, and 4 or 5 more in *aclis*.

14. Density of cephalic border nodes (minimum distance between adjacent nodes) [12:1]. 0: Separated by less than node diameter, 1: Separated by approximately node diameter, 2: Separated by more than node diameter.
15. Definition of nodes [12:1]. 0: Weakly defined, 1: Strongly defined.
16. Tubercles more strongly defined posteriorly than anteriorly [12:1]. 0: Absent, 1: Present, 2: Entirely absent or effaced anteriorly.
17. Border nodes more strongly defined anteriorly or absent posteriorly [12:1]. 0: Absent, 1: Present.
18. Unpaired sagittal anterior border node. 0: Absent, 1: Present.
19. Nodes inside posterolateral border furrow. 0: Absent, 1: Present.

A single pairs of low nodes are located inside the posterolateral angle of the cephalic border in *Meniscuchus menetus* and *Meniscuchus nanus*. These differ from the nodes recognised by Character 12 above by being separated from the border by a clear furrow. The homology of these two types of nodes cannot be demonstrated (although I consider it likely) and they are here treated as distinct pending further investigation. Öpik (1975, p. 30) compared the nodes of *Meniscuchus* type to those found in *Bolboparia*, which are here regarded as homologous with the border nodes of other taxa. However,

contrary to Öpik's assertion, the nodes of *Bolboparia* are clearly located on the cephalic border (see e.g. Rasetti 1966, pl. 5, figs 1, 4, 6, 13) and not inside it.

20. Cephalic border furrow effaced. 0: Absent, 1: Present.
21. Width of anterior border (sag.) in dorsal view as a proportion of cephalic length (sag.). 0: <0.10, 1 = 0.1-0.15, 2 = 0.15-0.2, 3 = 0.2-0.25, 4 = >0.25.
22. Border expanded sagittally so that a line perpendicular to the axis cuts the border furrow in four places. 0: Absent, 1: Present.
23. Degree of sagittal border expansion (width of border in dorsal view, sag., compared to width of border, exsag.) [22:1]. 0: Very small (less than 1.2 time exsag. width), 1: Small (1.2 to 1.5 times exsag. width), 2: Moderate (between 1.5 and 2 times exsag. width), 3: Large (greater than twice exsag. width).
24. Anterolateral cephalic border crescentic in dorsal view. 0: Absent (border slightly wider anteriorly than at 45 degrees, border as wide sagitally as at 45 degrees, or narrower sagitally than at 45 degrees), 1: Present (border at least 1.2 times wider sagitally than at 45 degrees).
25. Degree of anterior cephalic border expansion (length of border in dorsal view, sag., as a proportion of length of border at 45° between axis and posterior cephalic margin) [24:1]. 0: 1.2-1.5, 1: 1.51-1.9, 2: >1.9.
26. Cephalic border narrower (exsag.) anteriorly than posteriorly in dorsal view. 0: Absent, 1: Present.
27. Anterolateral cephalic border downsloping in lateral view. 0: Absent, 1: Present.
28. Pair of pores in anterolateral cephalic border. 0: Absent, 1: Present. [Autapomorphic for *Leptochilodiscus punctulatus*]
29. Shape of cephalon (sagittal length as a proportion of maximum width in dorsal view). 0: <=0.649, 1: 0.65-0.749, 2: 0.75-0.849, 3 >=0.85.
30. Anterior margin of cephalon truncated in dorsal view. 0: Absent, 1: Present.
31. Outline of cephalon two-phased (as described by Öpik 1975, p. 30). 0: Absent, 1: Present.
32. Shape of cephalic outline in dorsal view. 0: Semicircular (maximum width in posterior 0.25 of length), 1: Rounded (maximum width approximately at cephalic mid-length).
33. Width of cephalic border furrow (sag., in dorsal view). 0: Narrow (half or less than width of cephalic border), 1: Moderate (approximately equal in width to cephalic border), 2: Wide (over 1.5 times width of cephalic border).
34. Preglabellar field. 0: Absent (glabella reaches anterior border furrow), 1: Present.
35. Sagittal preglabellar furrow [32:1]. 0: Absent, 1: Present.
36. Width of sagittal preglabellar furrow [32:1]. 0: Wide (greater than or equal to half the width of the anterior glabellar lobe), 1: Moderate (approximately half the width of the anterior glabellar lobe), 2: Narrow (less than half the width of the anterior glabellar lobe).
37. Anterior genae crossed by transverse furrow at the position of the anterior termination of the glabella. 0: Absent, 1: Present.

A faint furrow is present in *Mallagnostus desideratus* (USNM 18327), that is similar to the stronger furrows seen in *Ladadiscus limbatus* (see Rushton 1966) and *Jinghediscus nummularius* (see Xiang and Zhang 1985, pl. 1, fig. 1).

38. Anterior genae with prominent caecal network. 0: Absent, 1: Present. [Autapomorphic for *Lenadiscus*]
39. Genae independently convex in anterior view. 0: Absent, 1: Present.
40. Genae overhanging border anterolaterally in dorsal view. 0: Absent, 1: Present.

Whilst the border furrow is effaced in *Analox*, the course of the furrow around the posterolateral corner of the cephalon shows that in this genus too the border is probably covered dorsally by the genae. The non-effaced posterolateral portion of the border furrow runs for a short distance under the convexity of the lateral margin of the cephalon (see Rasetti 1966, pl. 6, figs 3, 7).

41. Facial sutures. 0: Present, 1: Absent.
42. Palpebral lobes. 0: Present, 1: Absent.
43. Palpebral lobes strongly elevated above genae [42:0]. 0: Present, 1: Absent.
44. Palpebral furrows [42:0]. 0: Present, 1: Absent.
45. Width of palpebral furrows [44:0]. 0: Narrow, 1: Wide (subequal in width to palpebral lobes in dorsal view).
46. Length of palpebral lobes [42:0]. 0: Short (max. length of lobes less than 0.2 of the sag. length of cephalon, in dorsal view), 1: Moderate (0.2-0.29 of length of cephalon), 2: Long (0.3 or more of length of cephalon).
47. Shape of palpebral lobes (length of lobe as a proportion of width of lobe, in dorsal view) [42:0]. 0: 1-1.9, 1: 2-2.9, 2: 3-3.9, 3: 4-4.9, 4: 5-5.9, 5: 6+.
48. Anteroposterior position of palpebral lobes(distance from base of cephalon to midpoint of lobes as a proportion of length of cephalon, in dorsal view) [42:0]. 0: <0.3, 1: 0.3-0.39, 2: 0.4-0.49, 3: >=0.5.
49. Lateral position of palpebral lobes [42:0]. 0: At cephalic border (external margin of palpebral lobe in contact with cephalic border furrow, in dorsal view), 1: Inside cephalic border.
50. Angle of palpebral lobes to sagittal line [42:0]. 0: Parallel or subparallel, 1: Angled inwards (> 15 degrees).
51. Eye ridges. 0: Absent, 1: Very weak, 2: Well defined.
52. Width of eye ridges [51:1 or 2]. 0: Wide (maximum width greater than half maximum width of palpebral lobes), 1: Narrow (less than half maximum width of palpebral lobes).
53. Length of glabella (sag. distance from base of cephalon to anterior termination of the glabella) as a proportion of sag. cephalic length (excluding anterior border), in dorsal view. 0: <0.65, 1: 0.651-0.75, 2: 0.751-0.85, 3: 0.851-0.95, 4: >0.95.
54. Maximum width of glabella as a proportion of maximum width of cephalon (trans., in dorsal view). 0: <0.2, 1: 0.2-0.29, 2:0.3-0.39, 3: =>0.4.

55. Cephalic axial furrows effaced on external surface. 0: Absent, 1: Present.

56. Form of occipital ring. 0: Vertical, 1: Angled posteriorly.

57. Posterior of glabella inflated. 0: Absent, 1: Dorsally, 2: Posterodorsally.

58. Form of SO. 0: Approximately even width across entire axis, 1: Weaker medially than laterally, 2: Divided.

59. Length of divided SO furrows [58:2]. 0: Long, 1: Short.

60. SO furrows bifid. 0: Absent, 1: Present.

61. Weak furrow crosses posterodorsal glabellar expansion dorsally [57:2]. 0: Absent, 1: Present.

62. SO evenly effaced on external surface. 0: Absent, 1: Moderately effaced, 2: Entirely effaced.

63. SO consisting of pits isolated from axial furrows connected by narrow (sag.) furrow. 0: Absent, 1: Present.

64. Occipital spine or node. 0: Absent, 1: Present.

65. Cranidial spine (following Jell, 1975, p. 4): 0: Absent, 1: Present.

66. Form of cranidial spine [65:1]. 0: Long and strongly directed posteriorly, 1: Short and posterodorsally directed.

67. Occipital ring with strongly convex posterior margin compared to anterior margin. 0: Absent, 1: Present.

68. Basal lobes divided from median band of occipital ring. 0: Absent, 1: Present.

69. Pre-occipital glabellar spine or node (in holaspid). 0: Absent, 1: Present.

70. Long glabellar spine angled posterodorsally. 0: Absent, 1; Present.

71. Lateral furrows indicated by rounded pits isolated from axial furrows. 0: Absent, 1: Present.

72. S2 furrows entirely effaced. 0: Absent; 1: Present.

73. S2 furrows transglabellar. 0: Absent, 1: Weakly, 2: Strongly.

74. S3 furrows entirely effaced. 0: Absent, 1: Present.

75. S3 furrows transglabellar. 0: Absent, 1: Weakly, 2: Strongly.

76. Transglabellar S2 and S3 furrows merged medially [73: 1 or 2 and 75: 1 or 2]. 0: Absent, 1: Present.

77. Anterior glabella lobe expanded laterally (maximum width of lobe greater than posterior width of lobe). 0: Present, 1: Absent.

78. Anterior termination of glabella pointed. 0: Absent, 1: Present.

79. Anterior termination of glabella truncated: 0: Absent, 1: Present.

80. Angle of posterior axial furrows. 0: Strongly convergent anteriorly, 1; Weakly convergent or parallel, 2: Divergent anteriorly.

81. Number of thoracic segments. 0: 3, 1: 2.

Coding of all thoracic characters for *Opsidiscus microspinus* and *Macannaia maladensis* is based on the similar taxa *Opsidiscus brevicaudatus* (Jell 1975, p. 78, pl. 26, figs 1-2; pl. 28, figs 4-8), and *Macannaia stenorhachis* (Jell 1975, p. 73, pl. 25, figs 1-14), respectively.

82. Long axial spine on posterior thoracic segment. 0: Absent, 1: Present.

83. Thoracic axial spine geniculate [82:1]. 0: Absent, 1: Present.

84. Axial tubercles on thoracic segments. 0: Absent, 1: Present.

85. Anterior thoracic segment with long pleural spines. 0: Absent, 1: Present. [Autapomorphic for *Yukonia*]

86. Shape of pygidium (maximum width of pygidium as proportion of sag. length of pygidium, in dorsal view). 0: Long (<=1.4), 1: Intermediate (1.41-1.7), 2: Wide (1.71>=)

87. Width of pygidial border and furrow as a proportion of length of pygidium (sag., in dorsal view). 0: Very narrow (less than 0.05), 1: Narrow (0.05-0.09), 2: Wide (0.1-0.14), 3: Very wide (=>0.15).

88. Pygidial border furrow effaced. 0: Absent, 1: Present. [Autapomorphic for *Cephalopyge*]

89. Width of pygidial border increases posteriorly. 0: Absent, 1: Present.

90. Pygidial border with pair of dorsally directed marginal spines. 0: Absent, 1: Present. [Autapomorphic for *Lenadiscus*]

91. Pygidial border with segmental spines or serrations. 0: Absent, 1: Present.

The ventrally directed spines of *Serrodiscus*-like pygidia (see Jell *in* Bengtson *et al.* 1990; Rasetti 1966, p. 9) and the laterally directed border spines of other taxa (e.g. *Hebediscina sardoa*, Rasetti 1972, pl. 7, figs 5-20), which have a wide distribution amongst polymerids, are treated as homologous since both are likely to reflect the primitive segmentation of the pygidium.

92. Pygidial border spines all visible in dorsal view [91:1]. 0: Absent, 1: Present. [NA to taxa with 91:0]

The situation in *Leptochilodiscus*, where the posteriormost spine pair is visible in dorsal view but other spines are directed ventrally (see Rasetti 1967; Bassett, Owens and Rushton, 1976), is not considered to be homologous to that in other taxa. In *Leptochilodiscus*, the posterior spines are visible in dorsal view not due to their orientation with respect to the border but due to an upturning of the posterior part of the pygidial border.

93. Pygidial border doublure expanded and directed ventrally. 0: Absent, 1: Present.

This recognises the potential homology between the vertically directed spines of *Serrodiscus* and similar genera, and the 'cuff' of *Meniscuchus*, *Analox* and *Bathydiscus* (see Öpik 1975, p. 22). This is supported by the somewhat intermediate situation in *Litometopus*.

94. Doublure expanded around entire margin, with smooth or denticulate edge. 0: Absent, 1: Present.

95. Pygidial,border lowered postaxially. 0: Absent, 1: Present.

96. Pygidial border turned upwards postaxially. 0: Absent, 1: Present.

These two distinctive modifications of the pygidial border were recognised by Jell (1975, p. 86) in his phenetic analysis.

97. Pygidial axial furrows effaced externally. 0: Absent, 1: Present.

98. Width of pygidial axis as a proportion of maximum width of pygidum. 0: <0.25, 1: 0.25-0.29, 2: 0.3-0.34, 3: 0.35-0.39, 4: >= 0.4.

99. Pygidial axis short (less than 0.9 of the length of pygidium excluding border): 0: Absent, 1: Present.

100. Pygidial axis reaches border furrow. 0: Absent, 1: Present.

101. Pygidial axis overhangs border or border furrow posteriorly. 0: Absent, 1: Present.

102. Number of segments in pygidial axis. 0: 3, 1: 4, 2: 5, 3: 6, 4: 7, 5: 8, 6: 9, 7: 10, 8: 11, 9: >11.

In *Delgadella lenaicus* the number of rings can be coded, despite effacement of the furrows, because the segments are indicated by clear muscle scars. The number of segments in *Dicerodiscus* follows Jell's (1997, p. 389) observation of 3 pairs of pleural furrows, which appear to cover the length of the pygidium.

103. Pygidial ring furrows entirely effaced. 0: Absent, 1: Present.

104. Pygidial ring furrows effaced medially. 0: Absent, 1: Present.

105. Lateral margins of pygidial axis convex in dorsal view. 0: Absent, 1: Present.

106. Broad-based spine on more than one segment of pygidial axis, or encroaching on other segments. 0: Absent, 1: Present.

107. Angle of broad-based spine on pyigidial axis [106:1]. 0: Approximately vertical (greater than 70 degrees from horizontal), 1: Posterodorsally directed (30 degrees to 60 degrees from horizontal), 2: Posteriorly directed (less than 30 degrees).

108. Position of broad-based spine on pyigidial axis [106:1]. 0: anterior (less than 1/3 of axis length from anterior margin of pygidium), 1: Median (1/3-2/3 axis length), 2: Terminal.

109. Broad-based terminal spine incorporates terminal piece of pygidial axis [108:2]. 0: Absent, 1: Present.

110. Segmental spines or nodes on pygidial axis. 0: Absent, 1: Present.

111. Pygidial pleural furrows. 0: Present, 1: Absent.

112. Strength of pygidial pleural furrows [111:0]. 0: Strongly incised (deep furrows), 1: Weakly incised (relatively wide but shallow), 2: Faint (very narrow and shallow markings which do not interrupt pleural convexity).

113. Pygidial interpleural furrows. 0: Absent, 1: Present.

114. Pygidial pleurae overhang border and border furrow posterolaterally in dorsal view. 0, Absent, 1, Present.

115. Pygidial pleurae crossed by raised ridges that converge abaxially. 0: Absent, 1: Present. [Autapomorphic for *Lenadiscus*]

116. Punctate sculpture. 0: Absent, 1: Present.

117. Prominent tuberculate sculpture. 0: Absent, 1; Present.

118. Thoracic axis divided into lateral and median lobes. 0: Absent, 1: Present.

119. Articulating half-ring of anterior thoracic segments. 0: Present, 1: Absent.

120. Posterior part of pygidial axis unsegmented. 0: Absent, 1: Present.

121. Posterior margin of pygidium with pair of broad-based posteriorly directed spines. 0: Absent, 1: Present. [Autapomorphic for *Ptychagnostus*]

122. Anterior glabella effaced compared to posterior glabella. 0: Absent, 1: Present. [Autapomorphic for *Peronopsis*]

123. Thoracic axis more than half the width of the thoracic segment. 0: Absent, 1: Present.

Appendix 11. Synapomorphy scheme for nodes of the cladogram shown in Figure 4.9.

Character numbers, reconstructed changes, number of steps and character consistency indices are shown for each apomorphy. Characters and character states numbered as in the previous section and Table 9. Bold arrows '➔' under the 'change' column indicate unambiguous changes, light arrows '→' indicate ambiguous changes. Node numbers and six letter taxon codes, used to define branches are explained in Fig. 4.9 and Table 9, respectively.→

Branch	Character No.	Steps	Character CI	Change
Root → Node 79	14	1	0.500	0 → 2
	50	1	0.167	0 → 1
	51	1	0.364	1 → 2
	80	1	0.263	0 → 1
	87	1	0.405	1 → 2
	98	1	0.686	0 → 3
Node 79 → Node 78	1	1	0.167	0 → 1
	25	1	0.111	0 → 1
	34	1	0.071	1 ➔ 0
	47	1	0.500	0 → 1
	48	1	0.600	0 ➔ 3
	53	1	0.646	0 → 3
	56	1	0.200	1 ➔ 0
	57	1	0.250	2 ➔ 0
Node 78 → Node 76	54	1	0.714	1 → 2
	67	1	0.200	0 ➔ 1
	77	1	0.100	0 ➔ 1
	99	1	0.125	1 ➔ 0
Node 76 → Node 75	23	1	0.500	0 → 1
	33	1	0.417	0 ➔ 2
	51	1	0.364	2 ➔ 1
	53	1	0.646	3 → 2
	72	1	0.100	0 → 1
	91	1	0.091	0 ➔ 1
Node 75 → Node 73	24	1	0.077	0 ➔ 1
	48	1	0.600	3 ➔ 1
	50	1	0.167	1 ➔ 0
	74	1	0.143	0 → 1
	79	1	0.250	0 → 1
	102	1	0.632	1 → 0
Node 73 → Node 39	6	1	0.936	0 → 1
	21	1	0.521	1 → 0
	25	1	0.111	1 → 2
	51	1	0.364	1 ➔ 0
	61	1	0.200	1 → 0
	86	1	0.542	1 → 0
	111	1	0.143	0 ➔ 1
Node 39 → Node 38	29	1	0.528	2 → 3
	33	1	0.417	2 ➔ 1
	44	1	0.143	0 ➔ 1
	54	1	0.714	2 ➔ 3
	62	1	0.438	0 ➔ 2
	91	1	0.091	1 ➔ 0
	97	1	0.333	0 ➔ 1
	102	1	0.632	0 ➔ 7
	103	1	0.100	0 ➔ 1
Node 38 → Node 35	21	1	0.521	0 → 1

	48	1	0.600	1 → 2
	50	1	0.167	0 → 1
	67	1	0.200	1 → 0
	100	1	0.200	0 → 1
	105	1	0.167	0 → 1
Node 35 → Node 34	25	1	0.111	2 → 0
	41	1	0.111	0 → 1
	42	1	0.333	0 → 1
	52	1	0.167	0 → 1
	56	1	0.200	0 → 1
	79	1	0.250	1 → 0
	87	1	0.405	2 → 0
Node 34 → Node 31	33	1	0.417	1 → 0
	53	1	0.646	2 → 4
	97	1	0.333	1 → 0
Node 31 → Node 29	24	1	0.077	1 → 0
	25	1	0.111	0 → 1
	62	1	0.438	2 → 0
	100	1	0.200	1 → 0
Node 29 → Node 27	5	1	1.000	0 → 1
	54	1	0.714	3 → 2
	103	1	0.100	1 → 0
Node 27 → Node 10	16	1	0.333	0 → 2
	32	1	0.500	0 → 1
	34	1	0.071	0 → 1
	36	1	0.364	0 → 2
	53	1	0.646	4 → 1
	87	1	0.405	0 → 3
	89	1	0.250	0 → 1
Node 10 → Node 8	69	1	0.200	0 → 1
	74	1	0.143	1 → 0
	81	1	0.167	0 → 1
	102	1	0.632	7 → 8
Node 8 → Node 7	13	1	0.625	1 → 0
	27	1	0.200	0 → 1
	57	1	0.250	0 → 2
	75	1	0.313	0 → 2
	77	1	0.100	1 → 0
	98	1	0.686	3 → 4
Node 7 → Node 4	53	1	0.646	1 → 2
	84	1	0.250	0 → 1
	102	1	0.632	8 → 4
Node 4 → Node 3	1	1	0.167	1 → 0
	30	1	0.200	0 → 1
	104	1	0.083	0 → 1
Node 3 → Node 2	6	1	0.936	1 → 0
	68	1	0.500	0 → 1
	99	1	0.125	0 → 1
	106	1	0.100	0 → 1
	118	1	1.000	0 → 1
	119	1	1.000	0 → 1
	120	1	1.000	0 → 1
	123	1	1.000	0 → 1
Node 2 → ConAmi	64	1	0.125	0 → 1
	103	1	0.100	0 → 1
Node 2 → Node 1	3	1	0.200	0 → 1
	21	1	0.521	1 → 0
	72	1	0.100	1 → 0
	77	1	0.100	0 → 1
	87	1	0.405	3 → 2

	89	1	0.250	1 → 0
Node 1 → PerRod	1	1	0.167	0 → 1
	26	1	0.143	0 → 1
	84	1	0.250	1 → 0
Node 1 → PtyGib	35	1	0.250	0 → 1
	78	1	0.100	0 → 1
	82	1	0.333	0 → 1
	98	1	0.686	4 → 3
	104	1	0.083	1 → 0
Node 3 → TanBal	2	1	0.333	0 → 1
	22	1	0.077	0 → 1
	26	1	0.143	0 → 1
	34	1	0.071	1 → 0
	54	1	0.714	2 → 3
	81	1	0.167	1 → 0
Node 4 → TanAlt	72	1	0.100	1 → 0
	98	1	0.686	4 → (23)
	103	1	0.100	0 → 1
	105	1	0.167	1 → 0
Node 7 → Node 6	8	1	0.167	0 → 1
	69	1	0.200	1 → 0
	80	1	0.263	1 → 0
Node 6 → Node 5	1	1	0.167	1 → 0
	35	1	0.250	0 → 1
	68	1	0.500	0 → 1
	77	1	0.100	0 → 1
	78	1	0.100	0 → 1
	87	1	0.405	3 → 0
	89	1	0.250	1 → 0
	93	1	0.167	0 → 1
	94	1	0.250	0 → 1
	102	1	0.632	8 → 2
	110	1	0.071	0 → 1
Node 5 → CheAci	6	1	0.936	1 → 2
	21	1	0.521	1 → 0
Node 5 → CheCha	10	1	0.714	0 → 1
	75	1	0.313	2 → 1
	98	1	0.686	4 → 3
Node 6 → MinNum	12	1	0.091	0 → 1
	26	1	0.143	0 → 1
	27	1	0.200	1 → 0
	37	1	0.500	0 → 1
	62	1	0.438	0 → 1
	99	1	0.125	0 → 1
	103	1	0.100	0 → 1
Node 8 → MalLla	12	1	0.091	0 → 1
	72	1	0.100	1 → 0
	110	1	0.071	0 → 1
Node 10 → Node 9	26	1	0.143	0 → 1
	37	1	0.500	0 → 1
	99	1	0.125	0 → 1
Node 9 → MalDes	53	1	0.646	1 → 0
	62	1	0.438	0 → 2
Node 9 → MalLim	33	1	0.417	0 → 1
	54	1	0.714	2 → 1
Node 27 → Node 26	29	1	0.528	3 → 2
	77	1	0.100	1 → 0
	91	1	0.091	0 → 1
	93	1	0.167	0 → 1
	107	1	1.000	1 → 0

Node 26 → Node 25	13	1	0.625	1 → 0
	14	1	0.500	2 → 1
	21	1	0.521	1 → 2
	24	1	0.077	0 → 1
Node 25 → Node 22	25	1	0.111	1 → 2
	34	1	0.071	0 → 1
	53	1	0.646	4 → 3
	64	1	0.125	0 → 1
	105	1	0.167	1 → 0
	110	1	0.071	0 → 1
Node 22 → Node 21	12	1	0.091	0 → 1
	69	1	0.200	0 → 1
	72	1	0.100	1 → 0
	74	1	0.143	1 → 0
Node 21 → Node 13	1	1	0.167	1 → 0
	23	1	0.500	1 → 2
	25	1	0.111	2 → 0
	53	1	0.646	3 → 2
	63	1	0.250	0 → 1
	84	1	0.250	0 → 1
	102	1	0.632	7 → 9
	106	1	0.100	0 → 1
Node 13 → Node 12	6	1	0.936	1 → 2
	56	1	0.200	1 → 0
	92	1	0.250	1 → 0
	98	1	0.686	3 → 2
Node 12 → Node 11	4	1	0.333	0 → 1
	13	1	0.625	0 → 1
	29	1	0.528	2 → 3
	74	1	0.143	0 → 1
	87	1	0.405	0 → 1
	102	1	0.632	9 → 8
Node 11 → AciBir	14	1	0.500	1 → 2
	21	1	0.521	2 → 1
	25	1	0.111	0 → 1
	57	1	0.250	0 → 1
	106	1	0.100	1 → 0
Node 11 → AciThe	3	1	0.200	0 → 1
Node 12 → BolSup	14	1	0.500	1 → 0
	16	1	0.333	0 → 2
	22	1	0.077	0 → 1
	35	1	0.250	0 → 1
	39	1	0.125	0 → 1
	40	1	0.333	0 → 1
	64	1	0.125	1 → 0
	77	1	0.100	0 → 1
	78	1	0.100	0 → 1
	80	1	0.263	1 → 0
	110	1	0.071	1 → 0
	114	1	0.125	0 → 1
	117	1	0.200	0 → 1
Node 13 → StiSte	2	1	0.333	0 → 1
	12	1	0.091	1 → 0
	21	1	0.521	2 → 1
	29	1	0.528	2 → 1
	57	1	0.250	0 → 1
	58	1	0.583	0 → 1
	71	1	0.500	0 → 1
	105	1	0.167	0 → 1
	108	1	1.000	0 → 1

	111	1	0.143	1 → 0
Node 21 → Node 20	64	1	0.125	1 → 0
	73	1	0.625	0 → 1
	80	1	0.263	1 → 0
Node 20 → Node 19	15	1	0.500	0 → 1
	57	1	0.250	0 → 2
	75	1	0.313	0 → 2
	91	1	0.091	1 → 0
Node 19 → Node 15	13	1	0.625	0 → 2
	25	1	0.111	2 → 1
	70	1	0.333	0 → 1
	73	1	0.625	1 → 2
	93	1	0.167	1 → 0
	110	1	0.071	1 → 0
Node 15 → Node 14	16	1	0.333	0 → 1
	29	1	0.528	2 → 3
	102	1	0.632	7 → 5
	105	1	0.167	0 → 1
	106	1	0.100	0 → 1
Node 14 → AcmBil	1	1	0.167	1 → 0
	6	1	0.936	1 → 2
	12	1	0.091	1 → 0
	25	1	0.111	1 → 0
	63	1	0.250	0 → 1
	76	1	0.500	0 → 1
	80	1	0.263	0 → 1
	101	1	0.125	0 → 1
	117	1	0.200	0 → 1
Node 14 → SerGra	33	1	0.417	0 → 1
	34	1	0.071	1 → 0
	91	1	0.091	0 → 1
	93	1	0.167	0 → 1
Node 15 → SerDae	14	1	0.500	1 → 0
	18	1	0.333	0 → 1
	32	1	0.500	0 → 1
	58	1	0.583	0 → 2
	87	1	0.405	0 → 2
	89	1	0.250	0 → 1
Node 19 → Node 18	12	1	0.091	1 → 0
	17	1	0.500	0 → 1
	22	1	0.077	0 → 1
	34	1	0.071	1 → 0
	39	1	0.125	0 → 1
	40	1	0.333	0 → 1
	92	1	0.250	1 → 0
	94	1	0.250	0 → 1
	98	1	0.686	3 → 2
Node 18 → Node 16	21	1	0.521	2 → 4
	114	1	0.125	0 → 1
Node 16 → AnaBip	20	1	0.500	0 → 1
	23	1	0.500	1 → 3
	29	1	0.528	2 → 3
	62	1	0.438	0 → 1
	63	1	0.250	0 → 1
	70	1	0.333	0 → 1
	75	1	0.313	2 → 1
	76	1	0.500	0 → 1
	102	1	0.632	7 → 5
	105	1	0.167	0 → 1
	110	1	0.071	1 → 0

	116	1	0.200	0 → 1
Node 16 → NinStr	12	1	0.091	0 → 1
	18	1	0.333	0 → 1
	77	1	0.100	0 → 1
	101	1	0.125	0 → 1
Node 18 → Node 17	19	1	1.000	0 → 1
	31	1	1.000	0 → 1
	58	1	0.583	0 → 2
	95	1	0.500	0 → 1
	98	1	0.686	2 → 4
	100	1	0.200	0 → 1
	102	1	0.632	7 → 4
Node 17 → MenMen	22	1	0.077	1 → 0
	25	1	0.111	2 → 1
	73	1	0.625	1 → 2
	87	1	0.405	0 → 1
	101	1	0.125	0 → 1
Node 17 → MenNan	29	1	0.528	2 → 3
	75	1	0.313	2 → 1
Node 20 → SerSpe	13	1	0.625	0 → 3
	16	1	0.333	0 → 1
	62	1	0.438	0 → 1
	69	1	0.200	1 → 0
	87	1	0.405	0 → 1
Node 22 → SemSol	33	1	0.417	0 → 1
Node 25 → Node 24	3	1	0.200	0 → 1
	16	1	0.333	0 → 2
	81	1	0.167	0 → 1
	92	1	0.250	1 → 0
	103	1	0.100	0 → 1
	116	1	0.200	0 → 1
Node 24 → Node 23	7	1	1.000	0 → 1
	21	1	0.521	2 → 0
	24	1	0.077	1 → 0
	26	1	0.143	0 → 1
	30	1	0.200	0 → 1
	78	1	0.100	0 → 1
	96	1	1.000	0 → 1
	114	1	0.125	0 → 1
Node 23 → LepPun	34	1	0.071	0 → 1
	53	1	0.646	4 → 3
	67	1	0.200	0 → 1
	104	1	0.083	0 → 1
Node 23 → LepSuc	12	1	0.091	0 → 1
	40	1	0.333	0 → 1
	55	1	0.333	0 → 1
	63	1	0.250	0 → 1
	64	1	0.125	0 → 1
	77	1	0.100	0 → 1
	97	1	0.333	0 → 1
	102	1	0.632	7 → (89)
	110	1	0.071	0 → 1
Node 24 → LitLon	1	1	0.167	1 → 0
	6	1	0.936	1 → 2
	27	1	0.200	0 → 1
	29	1	0.528	2 → 1
	58	1	0.583	0 → 1
	86	1	0.542	0 → 1
	94	1	0.250	0 → 1
Node 26 → SerCte	1	1	0.167	1 → 0

	12	1	0.091	0 → 1
	17	1	0.500	0 → 1
	62	1	0.438	0 → (12)
	102	1	0.632	7 → 5
	104	1	0.083	0 → 1
	114	1	0.125	0 → 1
Node 29 → Node 28	1	1	0.167	1 → 0
	2	1	0.333	0 → 1
	27	1	0.200	0 → 1
	30	1	0.200	0 → 1
	58	1	0.583	0 → 2
	80	1	0.263	1 → 2
	87	1	0.405	0 → 2
	99	1	0.125	0 → 1
Node 28 → BatDol	22	1	0.077	0 → 1
	93	1	0.167	0 → 1
	94	1	0.250	0 → 1
	95	1	0.500	0 → 1
	98	1	0.686	3 → 4
Node 28 → OodSub	4	1	0.333	0 → 1
	6	1	0.936	1 → 2
	21	1	0.521	1 → 0
	34	1	0.071	0 → 1
	53	1	0.646	4 → 3
	57	1	0.250	0 → 2
Node 31 → Node 30	29	1	0.528	3 → 1
	102	1	0.632	7 → 4
	114	1	0.125	0 → 1
Node 30 → CobCom	80	1	0.263	1 → 0
	86	1	0.542	0 → 1
	104	1	0.083	0 → 1
	116	1	0.200	0 → 1
Node 34 → Node 33	34	1	0.071	0 → 1
	55	1	0.333	0 → 1
	80	1	0.263	1 → 0
	92	1	0.250	1 → 0
	98	1	0.686	3 → 4
Node 33 → CepNot	20	1	0.500	0 → 1
	27	1	0.200	0 → 1
	29	1	0.528	3 → (12)
	116	1	0.200	0 → 1
Node 33 → Node 32	12	1	0.091	0 → 1
	53	1	0.646	2 → 3
	77	1	0.100	1 → 0
	91	1	0.091	0 → 1
	93	1	0.167	0 → 1
	100	1	0.200	1 → 0
Node 32 → RunInd	21	1	0.521	1 → 0
	114	1	0.125	0 → 1
Node 32 → WeyNob	16	1	0.333	0 → 2
	87	1	0.405	0 → 2
Node 35 → HbsAtt	21	1	0.521	1 → 2
	51	1	0.364	0 → (12)
	64	1	0.125	0 → 1
Node 38 → Node 37	34	1	0.071	0 → 1
	43	1	0.143	0 → 1
	47	1	0.500	1 → 3
	53	1	0.646	2 → 3
	55	1	0.333	0 → 1
	77	1	0.100	1 → 0

	78	1	0.100	0 → 1
	80	1	0.263	1 → 0
	87	1	0.405	2 → 1
Node 37 → Node 36	98	1	0.686	3 → 1
Node 36 → DelCau	46	1	0.313	1 → 2
Node 36 → DelLen	25	1	0.111	2 → 0
	29	1	0.528	3 → 2
	114	1	0.125	0 → 1
Node 37 → DelAmo	24	1	0.077	1 → 0
	29	1	0.528	3 → 1
Node 39 → NeoDen	53	1	0.646	2 → 1
	86	1	0.542	0 → 2
	87	1	0.405	2 → 3
Node 73 → Node 72	35	1	0.250	0 → 1
	47	1	0.500	1 → 0
	98	1	0.686	3 → 2
	104	1	0.083	0 → 1
	113	1	0.167	1 → 0
Node 72 → Node 70	21	1	0.521	1 → 2
	29	1	0.528	2 → 1
	33	1	0.417	2 → 1
	46	1	0.313	1 → 0
	48	1	0.600	1 → 2
	67	1	0.200	1 → 0
	79	1	0.250	1 → 0
	112	1	0.308	0 → 2
Node 70 → Node 69	24	1	0.077	1 → 0
	25	1	0.111	1 → 0
	39	1	0.125	0 → 1
	52	1	0.167	0 → 1
	56	1	0.200	0 → 1
	57	1	0.250	0 → 2
	58	1	0.583	0 → 2
	65	1	0.333	0 → 1
	102	1	0.632	0 → 2
	106	1	0.100	0 → 1
Node 69 → Node 67	29	1	0.528	1 → 2
	43	1	0.143	0 → 1
	46	1	0.313	0 → 1
	53	1	0.646	2 → 1
	72	1	0.100	1 → 0
	74	1	0.143	1 → 0
	104	1	0.083	1 → 0
	108	1	1.000	0 → 2
Node 67 → Node 65	34	1	0.071	0 → 1
	54	1	0.714	2 → 1
	98	1	0.686	2 → 1
	106	1	0.100	1 → 0
	110	1	0.071	0 → 1
Node 65 → Node 60	10	1	0.714	0 → 2
	22	1	0.077	0 → 1
	24	1	0.077	0 → 1
	47	1	0.500	0 → 1
	48	1	0.600	2 → 1
	61	1	0.200	1 → 0
Node 60 → Node 58	44	1	0.143	0 → 1
	87	1	0.405	2 → 1
	91	1	0.091	1 → 0
	102	1	0.632	2 → 3
	113	1	0.167	0 → 1

Node 58 → Node 54	8	1	0.167	0 → 1
	9	1	0.400	1 → 0
	22	1	0.077	1 → 0
	36	1	0.364	0 → 1
	47	1	0.500	1 → 3
	78	1	0.100	0 → 1
Node 54 → Node 44	41	1	0.111	0 → 1
	42	1	0.333	0 → 1
	51	1	0.364	1 → 0
	60	1	0.250	0 → 1
	112	1	0.308	2 → 0
Node 44 → Node 42	29	1	0.528	2 → 1
	33	1	0.417	1 → 0
	53	1	0.646	1 → 2
Node 42 → Node 40	75	1	0.313	0 → 1
	82	1	0.333	0 → 1
	98	1	0.686	1 → 0
Node 40 → AbaMin	25	1	0.111	0 → 1
	102	1	0.632	3 → 5
Node 40 → AbaPau	8	1	0.167	1 → 0
	22	1	0.077	0 → 1
	36	1	0.364	1 → 0
	39	1	0.125	1 → 0
	51	1	0.364	0 → 1
	78	1	0.100	1 → 0
	86	1	0.542	1 → 2
	87	1	0.405	1 → 2
Node 42 → Node 41	9	1	0.400	0 → 2
	34	1	0.071	1 → 0
	66	1	0.250	0 → 1
	81	1	0.167	0 → 1
	101	1	0.125	0 → 1
	110	1	0.071	1 → 0
	117	1	0.200	0 → 1
Node 41 → DawBoh	86	1	0.542	1 → 2
	98	1	0.686	1 → 3
	102	1	0.632	3 → 2
Node 41 → DawDaw	21	1	0.521	2 → 3
Node 44 → Node 43	10	1	0.714	2 → 1
	21	1	0.521	2 → 0
	36	1	0.364	1 → 2
Node 43 → EodBor	9	1	0.400	0 → 2
	21	1	0.521	0 → 1
	84	1	0.250	0 → 1
Node 43 → EodSca	24	1	0.077	1 → 0
	102	1	0.632	3 → (678)
	111	1	0.143	0 → 1
	116	1	0.200	0 → 1
Node 54 → Node 53	25	1	0.111	0 → 1
	81	1	0.167	0 → 1
	82	1	0.333	0 → 1
	83	1	1.000	0 → 1
	106	1	0.100	0 → 1
Node 53 → Node 49	9	1	0.400	0 → 1
	33	1	0.417	1 → 0
	75	1	0.313	0 → 1
	107	1	1.000	1 → 2
	109	1	1.000	0 → 1
Node 49 → Node 48	21	1	0.521	2 → 1
	29	1	0.528	2 → 1

	102	1	0.632	3 → 1
Node 48 → Node 47	10	1	0.714	2 → 1
	30	1	0.200	0 → 1
	41	1	0.111	0 → 1
	49	1	0.333	0 → 1
	106	1	0.100	1 → 0
	112	1	0.308	2 → 1
Node 47 → Node 46	21	1	0.521	1 → 0
	24	1	0.077	1 → 0
	26	1	0.143	0 → 1
	36	1	0.364	1 → 0
Node 46 → HelBit	49	1	0.333	1 → 0
	51	1	0.364	1 → 0
	53	1	0.646	1 → 2
	98	1	0.686	1 → 2
	101	1	0.125	0 → 1
	102	1	0.632	1 → 0
	106	1	0.100	0 → 1
	117	1	0.200	0 → 1
Node 46 → Node 45	43	1	0.143	1 → 0
	47	1	0.500	3 → 0
	75	1	0.313	1 → 2
Node 45 → OpsBil	47	1	0.500	0 → 2
Node 45 → OpsLon	8	1	0.167	1 → 0
	29	1	0.528	1 → 0
	54	1	0.714	1 → 0
	72	1	0.100	0 → 1
	78	1	0.100	1 → 0
	80	1	0.263	1 → 2
Node 47 → OpsMic	46	1	0.313	1 → 2
Node 48 → PagPro	11	1	0.333	0 → 1
	113	1	0.167	1 → 0
Node 49 → PagBoo	25	1	0.111	1 → 0
	36	1	0.364	1 → 2
	54	1	0.714	1 → 2
	101	1	0.125	0 → 1
	110	1	0.071	1 → 0
	111	1	0.143	0 → 1
Node 53 → Node 52	53	1	0.646	1 → 2
	59	1	0.500	0 → 1
	66	1	0.250	0 → 1
	113	1	0.167	1 → 0
Node 52 → MacMal	36	1	0.364	1 → 2
	61	1	0.200	0 → 1
	87	1	0.405	1 → 2
	101	1	0.125	0 → 1
	104	1	0.083	0 → 1
Node 52 → Node 51	22	1	0.077	0 → 1
	106	1	0.100	1 → 0
	112	1	0.308	2 → 0
Node 51 → Node 50	44	1	0.143	1 → 0
	60	1	0.250	0 → 1
	75	1	0.313	0 → 1
	102	1	0.632	3 → 4
Node 50 → PdsEle	112	1	0.308	0 → 2
Node 50 → NepRjo	23	1	0.500	1 → 2
	29	1	0.528	2 → 1
	48	1	0.600	1 → 2
	98	1	0.686	1 → 0
Node 51 → PdsFra	36	1	0.364	1 → 0

	47	1	0.500	3 → 1
Node 58 → Node 57	65	1	0.333	1 → 0
	72	1	0.100	0 → 1
	74	1	0.143	0 → 1
	87	1	0.405	1 → 3
	110	1	0.071	1 → 0
Node 57 → Node 56	21	1	0.521	2 → 4
	23	1	0.500	1 → 2
	44	1	0.143	1 → 0
	53	1	0.646	1 → 2
	86	1	0.542	1 → 0
Node 56 → Node 55	8	1	0.167	0 → 1
	22	1	0.077	1 → 0
	25	1	0.111	0 → 2
	33	1	0.417	1 → 0
	80	1	0.263	1 → 0
	87	1	0.405	3 → 1
	112	1	0.308	2 → 0
Node 55 → KisCri	9	1	0.400	1 → 2
	29	1	0.528	2 → 1
	45	1	0.333	0 → 1
	53	1	0.646	2 → 3
	101	1	0.125	0 → 1
Node 55 → SpaJin	21	1	0.521	4 → 3
	44	1	0.143	0 → 1
	46	1	0.313	1 → 2
	48	1	0.600	1 → 2
	54	1	0.714	1 → 2
	102	1	0.632	3 → 2
	111	1	0.143	0 → 1
Node 56 → NatInc	29	1	0.528	2 → 3
	56	1	0.200	1 → 0
	57	1	0.250	2 → 0
	58	1	0.583	2 → (01)
	62	1	0.438	0 → (12)
	67	1	0.200	0 → 1
	100	1	0.200	0 → 1
Node 57 → NatDil	52	1	0.167	1 → 0
	98	1	0.686	1 → 2
Node 60 → Node 59	23	1	0.500	1 → 0
	60	1	0.250	0 → 1
	86	1	0.542	1 → 0
	98	1	0.686	1 → 2
	112	1	0.308	2 → 1
Node 59 → HbiSar	33	1	0.417	1 → 2
	34	1	0.071	1 → 0
	39	1	0.125	1 → 0
	43	1	0.143	1 → 0
	46	1	0.313	1 → 2
	51	1	0.364	1 → 2
	52	1	0.167	1 → 0
Node 59 → HbiYuq	25	1	0.111	0 → 1
	66	1	0.250	0 → 1
	102	1	0.632	2 → 4
Node 65 → Node 64	21	1	0.521	2 → 0
	33	1	0.417	1 → 2
	36	1	0.364	0 → 1
	66	1	0.250	0 → 1
Node 64 → Node 63	41	1	0.111	0 → 1
	43	1	0.143	1 → 0

	46	1	0.313	1 → 0
	59	*1*	*0.500*	*0 → 1*
	60	1	0.250	0 → 1
	102	1	0.632	2 → 3
Node 63 → Node 62	50	1	0.167	0 → 1
	71	1	0.500	0 → 1
	75	1	0.313	0 → 1
	79	1	0.250	0 → 1
	86	1	0.542	1 → 2
Node 62 → Node 61	24	1	0.077	0 → 1
	29	1	0.528	2 → 1
	33	1	0.417	2 → 1
	41	1	0.111	1 → 0
Node 61 → EgyWil	21	1	0.521	0 → 2
	22	1	0.077	0 → 1
	25	1	0.111	0 → 1
	47	1	0.500	0 → 1
Node 61 → EgyObt	91	1	0.091	1 → 0
	112	1	0.308	2 → 0
Node 62 → EgyZai	42	1	0.333	0 → 1
Node 63 → YudLac	8	1	0.167	0 → 1
	34	1	0.071	1 → 0
	39	1	0.125	1 → 0
	45	1	0.333	0 → 1
	61	1	0.200	1 → 0
	99	1	0.125	0 → 1
Node 64 → HbiBla	52	1	0.167	1 → 0
	87	1	0.405	2 → 3
Node 67 → Node 66	11	1	0.333	0 → 1
	47	1	0.500	0 → 2
	48	1	0.600	2 → 0
	87	1	0.405	2 → 1
Node 66 → EkwMar	24	1	0.077	0 → 1
	104	1	0.083	0 → 1
Node 66 → EkwPli	26	1	0.143	0 → 1
	102	1	0.632	2 → 1
	103	1	0.100	0 → 1
Node 69 → Node 68	21	1	0.521	2 → 0
	86	1	0.542	1 → 2
	99	1	0.125	0 → 1
Node 68 → AlaSpi	33	1	0.417	1 → 2
	39	1	0.125	1 → 0
	46	1	0.313	0 → 2
	47	1	0.500	0 → (23)
	81	1	0.167	0 → 1
	87	1	0.405	2 → 1
	103	1	0.100	0 → 1
	113	1	0.167	0 → 1
Node 68 → YuiInt	29	1	0.528	1 → 0
	41	1	0.111	0 → 1
	45	1	0.333	0 → 1
	48	1	0.600	2 → 3
	50	1	0.167	0 → 1
	54	1	0.714	2 → 1
	61	1	0.200	1 → 0
	78	1	0.100	0 → 1
Node 70 → PsePul	41	1	0.111	0 → 1
	53	1	0.646	2 → 3
	80	1	0.263	1 → 0
Node 72 → Node 71	43	1	0.143	0 → 1

	62	1	0.438	0 → 1
	64	1	0.125	0 → 1
	74	1	0.143	1 → 0
Node 71 → DicTsu	4	1	0.333	0 → 1
	21	1	0.521	1 → 3
	29	1	0.528	2 → 0
	30	1	0.200	0 → 1
	41	1	0.111	0 → 1
	50	1	0.167	0 → 1
	78	1	0.100	0 → 1
	80	1	0.263	1 → 0
	91	1	0.091	1 → 0
Node 71 → LuvGam	44	1	0.143	0 → 1
	46	1	0.313	1 → 2
	47	1	0.500	0 → 2
	72	1	0.100	1 → 0
	102	1	0.632	0 → 4
	112	1	0.308	0 → 1
	114	1	0.125	0 → 1
Node 75 → Node 74	46	1	0.313	1 → 0
	52	1	0.167	0 → 1
	54	1	0.714	2 → 1
	87	1	0.405	2 → 3
Node 74 → CalLob	41	1	0.111	0 → 1
	47	1	0.500	1 → 0
	72	1	0.100	1 → 0
Node 74 → KorOce	39	1	0.125	0 → 1
	75	1	0.313	0 → 2
	110	1	0.071	0 → 1
Node 76 → TchNin	1	1	0.167	1 → 0
	3	1	0.200	0 → 1
	21	1	0.521	1 → 2
	22	1	0.077	0 → 1
	29	1	0.528	2 → 0
	64	1	0.125	0 → 1
	80	1	0.263	1 → 0
	86	1	0.542	1 → 2
	98	1	0.686	3 → (01)
	102	1	0.632	1 → 3
Node 78 → Node 77	21	1	0.521	1 → 0
	29	1	0.528	2 → 1
	33	1	0.417	0 → 1
	73	1	0.625	0 → 2
	75	1	0.313	0 → 2
	113	1	0.167	1 → 0
Node 77 → SinShi	80	1	0.263	1 → 0
	117	1	0.200	0 → 1
Node 77 → SinSub	46	1	0.313	1 → 2
	47	1	0.500	1 → 2
	87	1	0.405	2 → 3
Node 79 → LenUni	24	1	0.077	0 → 1
	49	1	0.333	0 → 1
	54	1	0.714	1 → 0
	65	1	0.333	0 → 1
	104	1	0.083	0 → 1
	111	1	0.143	0 → 1
Root → Node 83	13	1	0.625	1 → 2
	43	1	0.143	0 → 1
	46	1	0.313	1 → 2
	47	1	0.500	0 → 5

	53	1	0.646	0 → 2
	69	1	0.200	0 → 1
	70	1	0.333	0 → 1
	73	1	0.625	0 → 1
	75	1	0.313	0 → 1
Node 83 → Node 82	21	1	0.521	1 → 2
	48	1	0.600	0 → 2
	62	1	0.438	0 → 1
	86	1	0.542	1 → 2
	102	1	0.632	1 → 4
Node 82 → Node 81	11	1	0.333	0 → 1
	12	1	0.091	0 → 1
	18	1	0.333	0 → 1
	103	1	0.100	0 → 1
	112	1	0.308	0 → 2
Node 81 → Node 80	54	1	0.714	1 → 0
	87	1	0.405	1 → 0
Node 80 → TsuNiu	29	1	0.528	2 → 1
	46	1	0.313	2 → 1
	62	1	0.438	1 → 0
	87	1	0.405	0 → 2
	112	1	0.308	2 → 0
Node 80 → TsuAcl	3	1	0.200	0 → 1
	15	1	0.500	0 → 1
	44	1	0.143	0 → 1
	80	1	0.263	0 → 1
	86	1	0.542	2 → 0
	91	1	0.091	0 → 1
	99	1	0.125	1 → 0
	103	1	0.100	1 → 0
	104	1	0.083	0 → 1
Node 81 → TsuKai	48	1	0.600	2 → 1
	102	1	0.632	4 → (23)
	110	1	0.071	0 → 1
Node 82 → TsuLon	1	1	0.167	0 → 1
	22	1	0.077	0 → 1
	29	1	0.528	2 → 1
	51	1	0.364	1 → 0
	91	1	0.091	0 → 1
	104	1	0.083	0 → 1
Node 83 → TsuOri	24	1	0.077	0 → 1
	29	1	0.528	2 → 3
	33	1	0.417	0 → 1
	110	1	0.071	0 → 1
	111	1	0.143	0 → 1